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ANTAGONISME DES MICROORGANISMES DU SOL ENVERS *FUSARIUM OXYSPORUM* F. *LINI*, AGENT DE LA FLÉTRISSURE DU LIN[1]

PAR RENÉ-O. LACHANCE[2] ET C. PERRAULT[3]

Abstract

Nineteen bacteria and 11 actinomycetes isolated from various soils in which fiber flax had been grown in the Lower St. Lawrence district were found to be antagonistic to *Fusarium oxysporum* f. *lini*. Among the 11 organisms forming the largest inhibition zone on agar plates, six had a fungicidal action on the spores of *F. oxysporum* f. *lini* while the other five exerted a fungistatic action. Among the 19 antagonistic bacteria under trial, six induced a swelling of the germ tubes or the production of an appressoriumlike structure on agar. Greenhouse experiments have indicated that 15 bacteria and 11 actinomycetes offered a certain protection to seedlings some of which reached 6, 12, and sometimes 24 in. in height before showing any signs of wilting. The organisms evidently delayed the onset of wilt symptoms, but failed to protect the plants through their entire growth.

Introduction

La phytopathologie s'intéresse à la lutte biologique, particulièrement dans certains cas où, le pathogène venant du sol, aucun des moyens de lutte ordinaires ne se montre efficace. La production de variétés immunes ou résistantes est sans aucun doute la solution la plus facile aux problèmes que posent ces maladies. Toutefois, dans certains cas, le choix d'une variété est régi par d'autres considérations que celle des rendements, de la qualité ou même de la résistance aux maladies. C'est le cas du lin à filasse dans la province de Québec. Depuis la fin de la guerre, la culture du lin à filasse a perdu de sa popularité à cause des prix avilis de la filasse et de l'étoupe. Pour tirer un revenu intéressant de cette culture, les producteurs doivent vendre la graine comme semence et non pour l'huile. Or, le marché d'exportation a des exigences spécifiques quant aux variétés, et il se trouve que les variétés en demande sur le marché d'exportation sont sujettes à la flétrissure, maladie causée par un champignon dont l'habitat normal est le sol.

[1] *Manuscrit reçu le 18 février, 1953.*
Contribution N° 1260 de la Division de la Botanique et de la Phytopathologie, Service des Sciences, Ministère de l'Agriculture, Ottawa, Canada.

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Dans un article antérieur (7), le premier auteur a rapporté quelques-uns des travaux qu'il a poursuivis sur l'antagonisme des microorganismes de sol envers le *Colletotrichum linicola*. Le présent travail porte sur la flétrissure du lin, maladie due à un champignon du sol et contre laquelle il n'existe pas de moyen de lutte adéquat. Il a semblé à propos d'explorer les possibilités d'une lutte biologique contre ce fléau.

Revue de la littérature

Chudiakov (2) a suggéré en 1935 que l'abondance de Fusarium dans les sols (à lin) malades résulte de l'absence, dans ces sols, de bactéries capables de produire une lyse des Fusariums. Lorsqu'il a introduit des Fusariums dans des sols contenant de telles bactéries, ils n'ont pu s'y développer et cet ensemencement artificiel n'a pas été suivi d'une infection des plantes.

Novogrudsky (9) affirme que l'inoculation d'un sol infecté avec des bactéries lysogènes a diminué d'une façon remarquable le pourcentage de plantes malades.

Novogrudsky *et al.* (10) et Berezova et Naumova (1), pour leur part, ont rapporté que la bactérisation de graines de lin infectées de divers parasites, y compris *Fusarium* sp., a réduit sensiblement le nombre de plantes malades.

Tervet (13) obtint des réactions différentes suivant qu'il utilisa une lignée faible ou une lignée virulente de *Fusarium lini*, en mélange avec plusieurs champignons agents de pourriture des racines. Avec une lignée faible, l'émergence était retardée de même que le flétrissement. Lorsqu'il utilisait une lignée virulente de *Fusarium lini* en présence d'une espèce de *Chaetomium*, la plupart des tiges de lin étaient encore vivantes après 24 jours. Leur système radiculaire était difforme avec des racines latérales courtes et renflées, rappelant un peu les mycorrhizes de *Pinus*, les entre-nœuds très courts, et le feuillage vert foncé. De ces plantes, un tiers ont survécu jusqu'à la floraison, mais elles étaient très rabougries.

Des tentatives ont été faites par Porter (11) pour protéger les semis de lin contre les attaques du *Fusarium lini*, en inoculant le sol avec une bactérie qui possédait, *in vitro*, un pouvoir inhibiteur extrême vis-à-vis ce pathogène. Ce chercheur a noté, au cours de ses expériences, que toutes les plantes avaient éventuellement succombé à la flétrissure bien que les témoins aient flétri plus tôt. Il a également trouvé qu'il fallait introduire les bactéries dans un bouillon de bœuf et non pas simplement en suspension dans l'eau pour que l'inoculation soit efficace.

Méthodes expérimentales et résultats

Les travaux poursuivis comprennent des expériences en serre et en laboratoire. Les essais *in vitro* visaient à déterminer la valeur de divers microorganismes isolés de certains sols de la province de Québec comme antagonistes à *F. oxysporum* f. *lini*. Les bactéries et sept des Actinomycètes mis à l'épreuve avaient été isolés au cours d'études sur l'anthracnose du lin rapportées dans l'article déjà cité (7): les six autres Actinomycètes ont été isolés

subséquemment. Conséquemment, un des trois milieux suivants fut utilisé pour déterminer le pouvoir antagoniste des organismes étudiés: la gélose aux pommes de terre, la gélose à l'oignon, ou la gélose nutritive sans dextrose. Vingt-neuf bactéries et treize Actinomycètes furent essayés en boîtes de Pétri sur le milieu qui convenait le mieux à chacun d'eux. Après vingt-quatre heures d'incubation, on inocula de nouveau chacune des boîtes en y vaporisant une suspension de spores de *F. oxysporum* f. *lini* dans de l'eau stérile. Cinq jours après, la zone d'inhibition produite variait d'un à dix-huit millimètres de chaque côté de la strie bactérienne. Dix-neuf bactéries et onze Actinomycètes ont produit une zone d'inhibition bien définie.

Dans vingt et une des cultures, les spores situées dans la zone d'inhibition n'ont pas germé; dans les neuf autres, il y eut production d'un tube germinatif dépassant rarement cinquante microns de longueur.

Quatre des dix-neuf bactéries mises à l'essai ont provoqué des renflements des tubes germinatifs à intervalles irréguliers, tout à fait comparables à ceux qu'avaient provoqué certains antagonistes chez *Colletotrichum linicola* (7) et analogues aux anomalies observées par Porter (11) chez *Helminthosporium*. Deux autres ont provoqué la formation d'un appressoire ou d'une structure analogue.

Cependant, après quinze jours, le *Fusarium* avait progressivement envahi la zone d'inhibition dans plus de la moitié des cultures. Ce phénomène ne peut être attribué à la germination retardée des spores situées dans la zone d'inhibition, ni à un regain de vie des tubes germinatifs dont la croissance aurait été momentanément suspendue par la toxicité de la substance sécrétée par l'antagoniste.

Nous avons déterminé la viabilité des spores situées dans la zone d'inhibition, en y prélevant des fragments de gélose contenant des spores de *Fusarium* et en les repiquant en tubes inclinés. Ces repiquages, faits trois et cinq jours après l'ensemencement des boîtes de Pétri avec *Fusarium*, nous ont permis d'établir que six des onze antagonistes mis à l'essai produisaient une substance fongicide; les cinq autres sécrétaient une substance fongistatique du fait que les spores, une fois transportées sur des tubes d'agar frais, reprirent leur croissance normale. Les autres organismes furent ignorés parce qu'ils ne produisaient pas de zone d'inhibition suffisamment large.

Les expériences *in vivo* ont été faites en serre. Pour inoculer le sol avec l'agent de la flétrissure, un mélange d'avoine et de blé stérilisé à l'autoclave a été ensemencé avec une suspension de spores de *F. oxysporum* f. *lini*. Après une bonne croissance du champignon, on mélangea l'inoculum au sol dans la proportion d'une partie pour trois parties de terre. On ensemença le sol ainsi inoculé une semaine plus tard seulement, afin de permettre au champignon de bien s'y établir.

Trois types de sol furent utilisés dans une première expérience: du terreau de serre, de la terre argileuse et de la terre graveleuse franche. Dans les expériences subséquentes, seul le terreau de serre fut utilisé, vu que les différences observées dans ces divers types de sols n'étaient pas significatives.

Il en fut de même des méthodes d'inoculation du sol avec les antagonistes. Dans la première expérience, les bactéries et les Actinomycètes furent introduits suivant deux méthodes, soit directement en vaporisant et mouillant le sol, sur une profondeur de trois pouces environ, avec une culture liquide des organismes à l'essai, soit indirectement en bactérisant la semence. Ces deux méthodes n'ayant donné aucune différence significative, seule la bactérisation de la semence fut utilisée dans les expériences subséquentes.

La méthode que l'on utilisa ressemble au procédé d'inoculation des semences de légumineuses. Une tourbe finement pulvérisée ayant un pH de 7.0 est stérilisée et inoculée avec les cultures liquides des antagonistes, en quantité suffisante pour porter l'humidité de la tourbe à quarante pour cent de son poids. La graine de lin est alors humectée et mélangée avec un excès de tourbe qui l'enrobe parfaitement et elle est semée immédiatement.

Les traitements ont été répétés quatre fois et distribués au hasard dans chacune des répétitions. Un pot de 6″ contenant approximativement 100 graines constitua un traitement. Tous les quinze jours, on arracha et compta les tiges malades.

Quinze bactéries et onze Actinomycètes furent mis à l'essai au cours de diverses expériences sur la bactérisation de la graine de lin. Bien que c'eût été préférable de les mettre à l'essai tous ensemble, il fut impossible de le faire, faute d'espace et d'autres facilités de travail.

Il ne semble pas nécessaire de présenter les résultats détaillés de toutes les expériences puisque, en définitive, elles ont toutes donné des résultats similaires. Les données d'une d'entre elles suffiront à démontrer qu'aucun des organismes utilisés n'a diminué le pourcentage de flétrissure. Comme les symptômes de la flétrissure peuvent se manifester à tout stade de croissance y compris les stades de préémergence et de maturité, les plantes furent conservées jusqu'à leur maturité. Pour toutes fins pratiques, on peut affirmer que, dans tous les pots et pour chacun des traitements, toutes les plantes succombèrent à la flétrissure. En fait, sur un total d'au moins 125,000 tiges manipulées au cours de ces expériences, trente-neuf seulement ont atteint la maturité sans flétrir. La graine de chacune de ces tiges fut conservée et semée plus tard dans une pépinière spécialement infectée, afin de vérifier s'il s'agissait de résistance réelle ou simplement de cas accidentels de non infection.

L'effet de la bactérisation de la semence avec les quinze bactéries et les onze Actinomycètes à l'étude a été de retarder l'apparition des symptômes de flétrissement, en comparaison avec les témoins. Le tableau I résume les résultats d'une expérience à trois différents stades de croissance, voire six pouces, douze pouces et vingt-quatre pouces de hauteur. Ces pourcentages ont été transformés, pour fins d'analyse statistique, en degrés angulaires d'après la table de Bliss reproduite par Snedecor (12). Ce tableau indique que les quatre organismes ont protégé les jeunes plantes et que trois d'entre eux ont retardé l'apparition des symptômes jusqu' à une période où ces plantes

TABLEAU I

EFFETS DE LA BACTÉRISATION DE LA SEMENCE SUR LE DEGRÉ D'INFECTION DU LIN À FILASSE

Antagonistes	Pourcentage de plantes flétries à divers stades de croissance		
	6 pouces	12 pouces	24 pouces
348	12.41* ± 1.75	17.25* ± 1.61	36.24 ± 1.64
418	12.76*	17.50*	38.44
419	12.25*	22.25	38.58
422	10.89*	16.75*	35.95
Témoin	18.24	25.50	38.43
D.R.S. p, 0.01	3.78	6.31	Test F non significatif
*Très significatif			

eurent atteint une hauteur de douze à vingt-quatre pouces. Toutes les plantes, tant dans les pots témoins que dans les pots traités, ont éventuellement succombé à la flétrissure avant d'arriver à maturité.

Fellows (3), Millard et Taylor (8), Garrett (4), King *et al.* (6) ont rapporté une diminution sensible de certaines maladies par simple addition, au sol, d'engrais verts ou de fumier de ferme. Ces chercheurs ont expliqué cette action, par l'activité accrue des microorganismes antagonistes aux agents pathogènes des plantes, grâce à l'apport de matière organique.

Il a paru intéressant de modifier la texture et surtout l'équilibre biologique du sol par l'apport d'engrais verts, afin de vérifier la possibilité de combattre le *Fusarium oxysporum* f. *lini* par ce moyen.

On utilisa de la terre argileuse déjà contaminée par le Fusarium. Trois espèces de légumineuses, la luzerne, le trèfle rouge et la fève soya furent choisis comme source de matière verte. Haché finement, l'engrais vert fut mélangé à raison d'une partie pour trois parties de terre. La graine de lin fut bactérisée et ensemencée une semaine plus tard et les mêmes organismes, qui avaient été utilisés dans l'expérience rapportée plus haut, furent mis à l'essai.

Les résultats furent aussi décevants que ceux des autres expériences. La bactérisation a retardé l'apparition des symptômes de flétrissure en comparaison avec le témoin non bactérisé, aussi bien dans les traitements avec les engrais verts que dans les traitements sans engrais, mais l'addition d'engrais vert n'a pas modifié la réaction, que la graine fut bactérisée ou non.

Discussion

La lutte biologique contre certaines maladies des plantes a déjà été abondamment étudiée et, dans certains cas, a donné des résultats prometteurs, surtout grâce à l'emploi d'engrais verts et d'engrais de ferme. Les chercheurs russes, tels Novogrudsky *et al.* (10), Berezova et Naumova (1), ont cependant tenté d'incorporer au sol des bactéries antagonistes à certains pathogènes du

lin et du blé et ont introduit le terme "bactérisation" pour décrire ce procédé. Toutefois, comme le souligne Jensen (5), les résultats que ces chercheurs ont obtenu devront être confirmés avant que la bactérisation des semences soit admise comme une méthode pratique de l'agriculture moderne. Dans le cas de la flétrissure du lin, les résultats bienfaisants de la bactérisation des semences rapportés par Chudiakov (2) et par Novogrudsky *et al.* (10) portent sur des jeunes plantes et les résultats rapportés ici pour des plantes environ du même âge concordent assez bien avec les leurs. Cependant, vu la nature du parasite qui peut attaquer le lin à tout stade de croissance et à cause de son habitat, toute expérience qui ne tient pas compte de ce fait est sujette à la critique et nos résultats confirment cet avancé. La bactérisation de la graine de lin a retardé l'apparition des symptômes de la flétrissure, mais n'a nullement empêché la maladie de tuer la totalité des plantes avant la maturité complète.

Berezova et Naumova (1) ont poussé leurs travaux plus loin et rapportent que la bactérisation a réduit de quinze pour cent le nombre de plantes atteintes de flétrissure au temps de la récolte et augmenté les rendements de dix à douze pour cent. Toutefois, une telle amélioration, même si elle est significative, ce qu'il est impossible de vérifier, ne justifierait pas le coût de la bactérisation de la semence dans le cas de la flétrissure fusarienne du lin.

La bactérisation des semences peut trouver des applications utiles pour les maladies qui ne s'attaquent qu'à des plantes jeunes qui, par la suite, acquièrent une résistance naturelle.

Résumé

Dix-neuf bactéries et onze Actinomycètes isolés de sols où se cultive le lin dans le Bas Saint-Laurent se sont avérés antagonistes *in vitro* à *Fusarium oxysporum* f. *lini*.

Six des onze organismes qui produisirent la plus grande zone d'inhibition eurent une action fongicide sur les spores de *F. oxysporum* f. *lini*, tandis que les cinq autres n'eurent qu'un effet fongistatique. Six des dix-neuf bactéries antagonistes ont provoqué, sur gélose, un renflement des tubes germinatifs ou la production d'appressoires ou de structures analogues.

Les études *in vivo* ont indiqué que l'inoculation du sol et la bactérisation de la semence avec quinze des bactéries et onze Actinomycètes à l'étude ont protégé le lin jusqu'à six et douze pouces de hauteur et parfois davantage, retardant ainsi l'apparition des symptômes de la flétrissure qui, tôt ou tard, se sont manifestés avant que les plantes eurent atteint leur pleine maturité.

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CYTOLOGICAL STUDIES OF CHROMOSOMES OF RUST FUNGI

I. THE MITOTIC CHROMOSOMES OF *PUCCINIA GRAMINIS*[1]

By R. C. McGinnis[2]

Abstract

Germinating sporidia (basidiospores) of *Puccinia graminis* Pers. were cytologically examined during nuclear division (mitosis) to determine the chromosome number. Studies at metaphase showed a haploid number of six chromosomes for this organism. Prophase chromosomes were observed to be united to form a continuous chain. Limits of individual chromosomes could not be seen at this stage. At metaphase, what were apparently residual terminal attractions were observed, the six chromosomes appearing as three loose pairs. The possibility of a basic chromosome number of three for this species is discussed.

Introduction

Many cytological investigations of the rust fungi have been made over the past 70 years. The actual study of chromosome number and behavior in the rusts, however, has received only limited attention. Since a knowledge of the nuclear components of any species is basic to a wider understanding of its genetics and phylogeny, a chromosome study of stem rust (*Puccinia graminis* Pers.) was undertaken.

Literature pertinent to the chromosomes of *Puccinia graminis* is lacking, and only limited researches have been reported for other species of the Uredinales. Of the early cytopathologists, Juel (6) in 1898 was unable to make a definite count but was convinced that there were more than two chromosomes at nuclear fusion in *Coleosporium campanulae.*

In 1902, Holden and Harper (5) observed six to eight chromosomes in the first division of the fusion nucleus of *C. sonchi-arvensis.* In another species, *C. tussilaginis,* Ashworth (2) made a count of from 8 to 10 haploid chromosomes, while Olive (8) reported a haploid number of eight in meiotic studies on *C. vernoniae.* Allen (1) suggested a probable haploid number of five for *Puccinia malvacearum* but later Savile (9) reported a count of four for this species. Savile (9) also observed a haploid number of four in *Uromyces fabae, U. hyperici, Puccinia sorghi,* and *Melampsora bigelowii.*

Materials and Methods

The studies herein reported were made on sporidia (basidiospores) of *Puccinia graminis* and are concerned with chromosomes of the haploid phase of that species, since meiosis occurs in the promycelia of the teliospores just prior to the formation of the sporidia. The sporidia were obtained from germinable teliospores on straws of *Agropyron trachycaulum* (Link) Malte collected at Winnipeg, Man. Sporidia were discharged over microscope slides for about 16 hr. The slides were then immersed in Carnoy's solution A(6 : 3 : 1) for fixing and smeared in aceto-orcein stain (3).

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Cytological examinations were made at a magnification of 1325×. Photomicrographs were taken at 900× as in Figs. 1 and 2, and 1080× as in Figs. 3 and 4. Further enlargements were made at the time of printing as described on Plate I.

Results

Because sporidia were discharged on each slide over a period of about 16 hr., it was possible to study sporidia at different stages of development from freshly discharged, ungerminated ones, to those having germ tubes up to 100 μ in length. Allen (1) in *Puccinia malvacearum* and Savile (9) in *P. malvacearum*, *Uromyces lespedezae-procumbentis*, and *Melampsora bigelowii* found that the basidiospore nucleus divided before germination of the spore. The present study showed a similar general behavior in *P. graminis*. Usually the binucleate condition existed prior to germ tube formation. In a low percentage of cells, however, germination was precocious and preceded nuclear division (see Fig. 3).

Examination of the chromosomes during the first nuclear division demonstrated a phenomenon not heretofore reported to the best of the writer's knowledge. At late prophase the chromosomes appeared to be attached in such a manner as to form a continuous chain or "spireme" (Figs. 1 and 2). During the course of this study five such cells were observed, leaving little doubt that this chromosome association, if not the normal condition, does at least occur frequently. It is believed that these cells were at late prophase. Fig. 1 shows a random arrangement of the "spireme" throughout the cell presumably because no polar forces were yet active. A slightly later prophase stage is shown in Fig. 2 where the forces of division have caused some orientation of the chromosomes to form a spiral arrangement. Limits of individual chromosomes could not be seen, the over-all length of the configuration being about 14 μ.

Since the sporidia are haploid and in the process of mitosis, the formation of these spireme-like structures is an interesting phenomenon. The possibility of actual chiasmatic union of chromosomes can be almost excluded since crossing-over—reported rarely in mitotic divisions in higher plants—could hardly involve all the chromosomes of the haploid rust organism. A second hypothesis might be that chromosomes in this organism form a true spireme. Early cytologists believed that a continuous thread of chromosomes or spireme was formed prior to chromosome differentiation in prophase. More recently this theory has been considered untenable. It is not proposed that the old conception be revived, but it is suggested that this study presents some evidence to support the existence of a spireme stage in mitotic prophase of this organism.

A third, and possibly more valid hypothesis, would be that of a chromosome union effected by end-to-end attractions of the chromosomes. Although not usually associated with mitosis, terminal attractions have been observed in

higher plants, particularly haploids, during meiosis, where up to five chromosomes have been found to be associated in this manner (7, 10). Several workers (4, 10, 11) have postulated that the attraction is due to genic or segmental homology between otherwise nonhomologous chromosomes, and is an indication of a lower basic chromosome number for a species. In some respects, meiotic haploid chromosomes are like mitotic chromosomes since there is ordinarily no synapsis in either case. Consequently, it could be postulated that in *P. graminis*, forces of attraction occur between segments of different chromosomes resulting in a closely connected chain. Furthermore, if attraction is between homologous or homoeologous segments of chromosomes, it might be indicative of a polyploid nature of the organism.

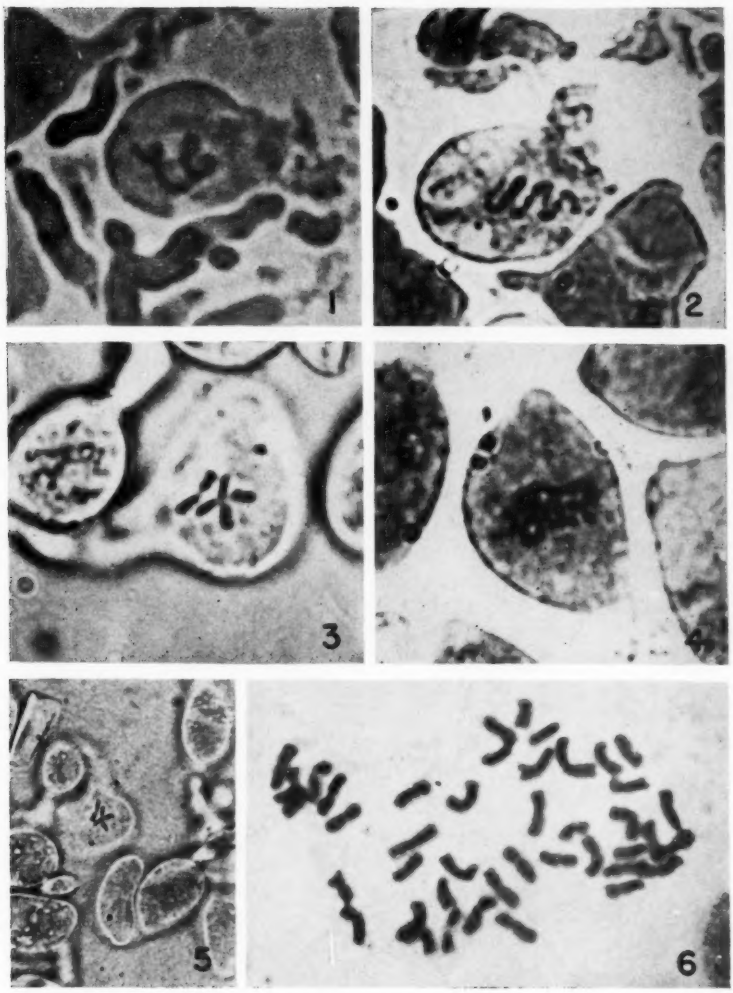
Six sporidia at metaphase had deeply stained chromosomes which were sufficiently distinct and spread that a reliable chromosome count could be made (Fig. 3). On the basis of the evidence obtained from these cells, the writer is convinced that *Puccinia graminis* has a haploid number of six chromosomes. A study of several other sporidia at the same stage of division gave no contradictory evidence, although a definite count of six could not be established in these sporidia.

All six chromosomes appeared to be of uniform size at metaphase but slight variations were noted between different cells. Measurements showed the chromosomes to be from 0.8 μ to 1.4 μ in length and about 0.3 μ to 0.5 μ in width. Figs. 5 and 6 serve to illustrate the relative size of mitotic chromosomes of *P. graminis* and *Triticum vulgare*, respectively.

It is surprising that more nuclei were not observed at the metaphase or early anaphase stage of division. Although no actual count was made, it is estimated that only about one cell in 5,000 to 10,000 cells was at metaphase or early anaphase. Probably this stage of division is of very short duration, perhaps lasting not more than a few seconds. The low frequency of metaphases indicates the necessity of studying a great deal of material.

A study of the metaphase chromosomes gave further evidence that stem rust is polyploid. In Fig. 3 it can be seen that the six chromosomes actually appear as three associations of two chromosomes. Although focusing showed the chromosomes to be clearly separated, residual terminal attractions did appear to be present. Similar configurations were observed in two other cells at the same stage of mitosis. Such pairing could be taken as further evidence that the prophase chromosomes do normally form a chain. The presence of the three loose pairs would signify greater terminal attractions between specific pairs of chromosomes. Thus, under the forces set up during division, the more weakly paired ends of the chromosomes would break away first in the "spireme", resulting in three semiunited pairs. If these "pairs" can be taken as evidence of relic homology, then it can be postulated that the basic chromosome number is three for this organism.

Three cells were observed at late metaphase. The chromosomes had split longitudinally, remaining joined only at the medial centromeres. All six chromosomes were completely separated with no apparent pairing attractions



Mitosis in sporidia of *Puccinia graminis*

FIG. 1. Continuous chain of chromosomes at prophase. Sporidium ungerminated. 2700×.

FIG. 2. Later prophase. Chromosomes still united but oriented at plate in a spiral arrangement. Sporidium ungerminated. 2700×.

FIG. 3. Early metaphase. The six chromosomes show residual terminal attractions to form three pairlike associations. Sporidium germinated. 2700×.

FIG. 4. Early anaphase showing probably 12 chromosomes. Sporidium ungerminated. 3200×.

FIGS. 5 AND 6. Chromosomes of *Puccinia graminis* and *Triticum vulgare*, respectively, both at 1200× demonstrating relative chromosome size. The cell in Fig. 5 is the same one as in Fig. 3.

which indicated that anaphase movement would progress in the conventional manner observed in higher plants. Unfortunately it was impossible to get well-spread anaphase preparations so that chromosome behavior at this stage could not be studied in detail. Fig. 4 shows the chromosomes at early anaphase to be much reduced in size from metaphase and although a definite count could not be established at this stage, there appeared to be 12 chromosomes.

Discussion

Because of its economic importance, the stem rust organism warrants more complete study in cytogenetic phases. Certainly a study of the chromosomes of any species is basic to a better understanding of such matters as inheritance and phylogeny.

A number of questions have been raised by this study. Firstly, the unusual spireme-like association of chromosomes at mitosis is very difficult to interpret and explain. If a similar complex configuration should occur at meiosis, what would be the effect on the genetic stability of the organism?

A second consideration is that of speciation of the organism. Should the basic chromosome number in *P. graminis* be three, then how is the present condition of six chromosomes to be explained? Was it accomplished simply through chromosome doubling, or did two distinctly different species contribute chromosomes to form an amphiploid? A chromosome study of other species and genera might throw some light on this subject.

A final major consideration is that of pathogenicity. Does the polyploid nature of the fungus—if such is actually the case—have any bearing on increased pathogenicity or wider host range? It has been observed frequently that polyploids are often better adapted to more varied conditions than the constituent species. Could this not also be true in the case of stem rust?

Acknowledgments

The writer wishes to express his appreciation to Dr. T. Johnson, Officer-in-Charge, Laboratory of Plant Pathology, Winnipeg, for suggesting the project and supplying the material used in this study, as well as for helpful suggestions throughout the course of the investigation. He is also indebted to Dr. R. F. Peterson, Officer-in-Charge, Laboratory of Cereal Breeding, Winnipeg, and to Dr. John Unrau, Professor of Plant Science, University of Alberta, for reading and criticizing the manuscript.

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OBSERVATIONS ON INTERPHASE AND PROPHASE NUCLEI OF ROOT TIPS OF EINKORN WHEAT AND ONION[1]

By Clayton Person[2]

Abstract

Studies of cells in interphase and prophase show that at all stages of the mitotic cycle in the nuclei of Einkorn wheat and onion root tips the arrangement of the chromosomes bears a definite relation to the axis of the nucleus. The establishment, by the centromeres, of the metaphase plate is described. The observations are compared with those of previous investigators and possible applications in other fields of investigation are suggested.

Introduction

At metaphase and through to telophase there is an organized arrangement of the chromosomes, and this organization is usually considered to be related to the spindle which is present during these stages. The disposition of the chromosomes and other components of the nucleus during interphase and prophase is not so easily observable, and it is not generally accepted that a state of organization exists through these stages when the spindle is absent. This study is, accordingly, confined to interphase and prophase nuclei. The results are compared with those of previous investigators and their possible applications in other lines of investigation are suggested.

Material and Methods

Untreated onion (*Allium cepa* L., $2n = 16$) and Einkorn (*Triticum monococcum* L., $2n = 14$) root tips, growing or germinated in the tap water, were fixed in Carnoy's solution (6 : 3 : 1) for 24 hr., hydrolyzed for 50 min. in a 1 : 1 : 2 solution of hydrochloric acid (conc.) – alcohol – water, washed, and stained in leucobasic fuchsin for 10–15 min. They were then immersed in a dilute solution of fast green in 45% acetic acid for three to four minutes and placed on a slide in a small drop of acetic acid. A cover slip was then applied, tapped gently, floated off in a 3 : 1 alcohol–acetic solution, and replaced using a drop of Euparol. The fast green rendered the nucleoli and cytoplasm more clearly visible.

Observations

In the meristematic cells of onion and Einkorn root tips the interphase nuclei were granular in appearance with a more densely staining region at one portion of the nuclear periphery. This was best observable in "lateral" views where the intensity of staining appeared to diminish from one side of the nucleus to the other (Figs. 1, 10). The nucleoli varied in number from one to four in different nuclei, and though the chromatin was obscured in these

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Contribution from the Department of Plant Science, University of Alberta, Edmonton, Alberta. This study was supported by the National Research Council of Canada in the form of a studentship.

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nucleolar regions, it was still possible to discern that the lighter staining on one side of the nucleus was not entirely due to the presence of the nucleoli.

The gradation in stain intensity persisted through prophase to shortly before metaphase (Figs. 4–6, 8–9, 12, 15–17). As prophase proceeded the nucleoli became progressively less distinct (Figs. 3–7, 9–10, 12, 16).

The chromosomes, when first recognizable, appeared coiled (Figs. 2–5). No single thread could be traced for any appreciable distance; they had, in some small regions, the appearance of doubleness but for the most part they were optically single. At a slightly later stage the chromosomes were thicker, more easily traceable for longer distances, and here they appeared as single coiled threads (Fig. 5). Though the orientation, locally, of the single threads appeared to be random the chromosomes as a group radiated from the densely stained to the weakly stained sides of the nucleus (Figs. 3–5). Terminal chromosome segments were occasionally observable at the light staining side of the nucleus, and these were traceable for short distances into the chromatin mass (Fig. 5). In mutilated nuclei parts of individual chromosomes were more clearly observable (Fig. 2).

In later prophase nuclei, chromosome coiling could no longer be seen (Figs. 6–7, 9–13, 15–17). The threads were thicker, shorter, again double in certain regions and showed a more or less parallel arrangement from the dark to the light sides of the nucleus (Figs. 10, 12–13, 15–16). In these the nucleoli were either more difficult to see or else completely invisible. In well flattened cells chromosome ends could be seen at the light side of the nucleus (Figs. 8–9, 12–13, 15–17) and at the darkly stained region the chromosomes were seen to be looped, the mid-points of the loops being concentrated in a very small area at or very near the surface of the nucleus (Figs. 12–17). In polar aspect the mid-points of the loops appeared to be arranged in the form of a circle (Figs. 11, 17).

In cells at a still later stage the chromosomes were clearly double, the chromatids were relationally coiled, and the loops of the chromosomes were still localized within a very small region (Figs. 14, 19, 21). In some cells the mid-points of the chromosome loops appeared to be arranged in the form of a circle at or near the nuclear periphery (Fig. 14). Lightly stained bands could sometimes be seen at the apices of the loops. These were presumed to be the centromeres. The chromosome ends were still directed toward the opposite side of the nucleus (Figs. 14, 18–21) although occasionally an end was seen extending randomly from the main group. As prophase continued an increasing number of cells showed one or several chromosome arms projecting away from the remainder (Figs. 22–24). In slightly earlier cells the nuclei had appeared spherical, and in some the chromosomes appeared to be arranged in the form of a hollow sphere (Figs. 11, 14, 16). It is possible that the nuclear membrane disappears at this time and releases the chromosomes from their spherical arrangement.

In later prophase nuclei (Figs. 3, 9, 22–24) the centromeres retained their association and their arrangement seemed not significantly different from that

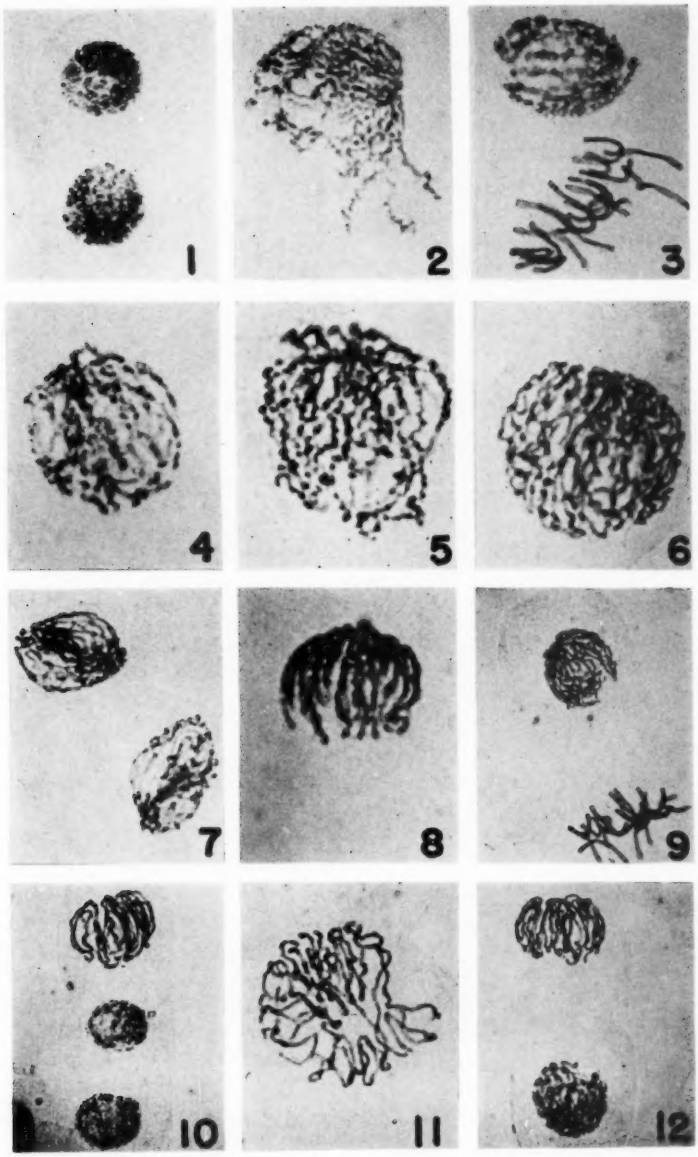

FIG. 8 is of an Einkorn cell, the rest of the figures are of onion.
For further description see text.

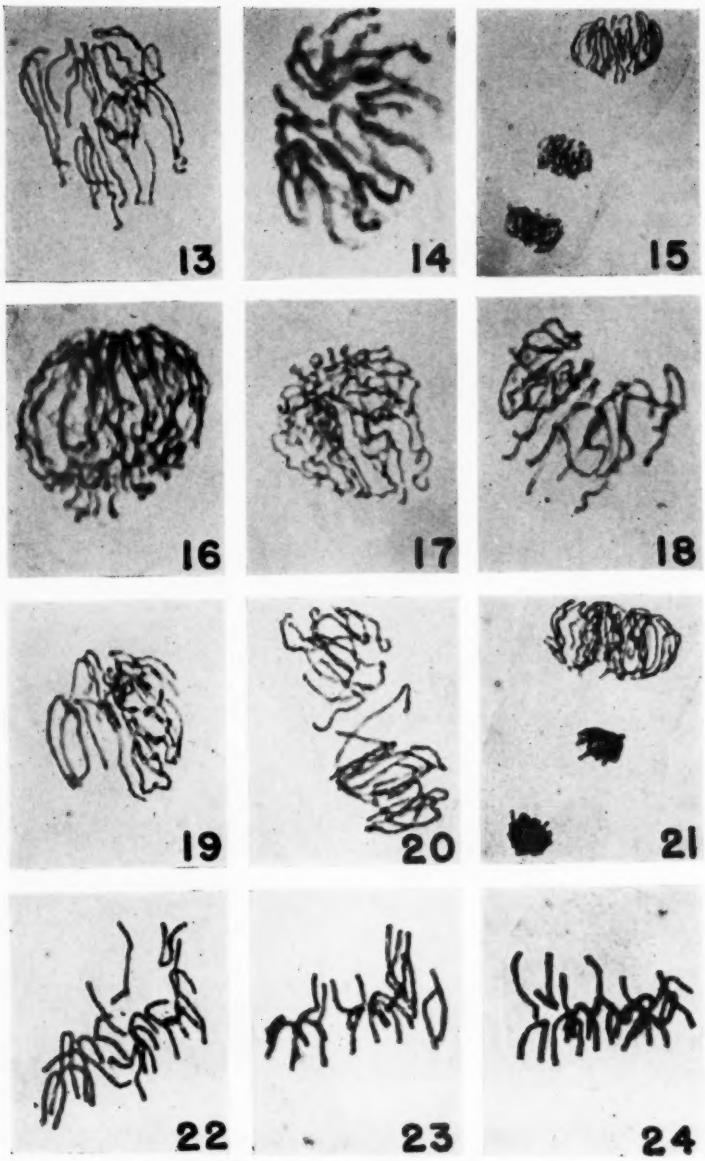

FIG. 14 is of an Einkorn cell, the rest of the figures are of onion.
For further description see text.

which is observable at metaphase. In these cells the chromosomes had still to reach the degree of contraction characteristic of metaphase and the majority of the chromosome ends were still oriented to one side of the "plate" (Figs. 3, 22–23). In other cells, where chromosome contraction was even further advanced, the chromosome orientation was still not random (Fig. 24).

In cells with centromeres at the metaphase plate the variability in chromosome orientation and chromosome contraction was such that a typical stage could not be selected to mark the end of prophase.

In Einkorn cells the midregions of the chromosomes appeared most densely stained (Figs. 8, 14) while in onion cells the chromosomes appeared uniformly stained throughout their length; in both, the tendency for one part of the early prophase nucleus to stain more darkly was considered due mainly to the concentration of the centromeres within a very small area at or near the nuclear membrane.

Discussion and Conclusions

Doutreligne (1) described, for interphase nuclei of the reticulate type, a densely staining "polar" region, in which the centromeres were located, and a weakly staining "antipolar" region, in which the distal ends of the chromosomes were located. She stated further that a careful analysis of the interphase nucleus reveals the existence of minute zigzag filaments oriented more or less parallel and united by fine anastomoses. The "filamentous-reticular" aspect of living interphase nuclei had been described earlier by Martens (2).

In the present study, where the staining differential observable at prophase was clearly related to the arrangement of the chromosomes, it is a reasonable assumption that the same holds true for the interphase nuclei, and this is in complete accord with the earlier observations. At all stages of the mitotic cycle the disposition of the chromosomes was as though they were arranged in definite relation to a nuclear axis. The centromeres, tightly grouped at late anaphase (Fig. 21) remain associated in the following prophase (densely staining areas, Figs. 4, 5) when they separate in the form of an enlarging ring to establish the metaphase plate (Figs. 11, 14). This establishment, by the centromeres, of the metaphase plate is completed before the stage usually designated as metaphase is reached.

A similar process in establishing the metaphase plate has been described for onion by Vanderlyn (4); he believed it was accompanied by a rotation of the nucleus so that the plane of metaphase comes to lie perpendicular to the long axis of the cell. Nuclear rotation during prophase has also been observed in living cells by Martens (2).

In this study the majority of prophase nuclei were oriented with the chromosomes in line with the long axis of the cell (Figs. 6, 10, 12–13, 15, 21, 24); the establishment of the metaphase plate in the appropriate plane therefore required no nuclear rotation. In many telophase cells the nuclei appeared to be in the process of rotating, and in many interphase and some prophase cells

it appeared that some rotation would be necessary if the metaphase plate were to become perpendicular to the long axis of the cell. It is concluded that if nuclear rotation does occur it is not limited to prophase.

Vanderlyn (4) believed that nuclear rotation was a manifestation of tissue polarity. The statement of Sinnott and Bloch (3) that "the first visible evidence of the polarity of the cells is thus provided by the cytoplasmic configuration rather than by the events in the nucleus" does not exclude a possible role of the nucleus in cell polarity. Further studies, using organisms whose nuclear polarity is clearly expressed, would doubtless yield more definite information on the individual action of the nucleus and cytoplasm in growth and differentiation.

Prophases similar to those described here have been observed by Martens (2) in nine species, by Doutreligne (1) in three species, and by the author in *Hordeum* and *Secale*. In all these species the nuclei are of the reticulate type. In plants with nuclei having a number of small deeply staining regions (euchromocenters or prochromosomes) the distribution of these regions is apparently apolar and prophase follows a different course of events (1). It is possible that the differences between these nuclear types—reticulate and euchromocentric—may be usefully exploited in experimentation using physiologically active substances which are known to affect polarity. It is also suggested that detailed studies of events during prophase in reticulate nuclei may be profitably considered when interpreting the later behavior of chromosomes following treatments which result in modified mitoses.

Acknowledgment

The author is grateful to Prof. John Unrau, of the University of Alberta, and to Prof. T. J. Arnason, of the University of Saskatchewan, for advice and criticism throughout the course of this study.

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THE EFFECTIVENESS OF CERTAIN FUNGICIDES AGAINST *BOTRYTIS TULIPAE* (LIB.) LIND[1]

By R. E. Sampson[2] and R. A. Ludwig[3]

Abstract

A number of methods reported to be effective in the production of spores of *Botrytis tulipae* gave unsuccessful results. Both macro- and microconidia were, however, obtained by growing the fungus on living tulip leaves and petals in moist chambers.

Comparisons *in vitro* showed thiram and ferbam to be effective against *Botrytis tulipae* at lower concentrations than either chloranil or Vancide 51. Sodium *o*-phenylphenate was intermediate at the LD_{50} point but its probit log concentration regression line was of steeper slope than those of thiram, ferbam, or chloranil which were parallel. This parallelism is a good indication that these compounds have a similar mechanism of action. These chemicals, when applied to infested tulip bulbs, did not control botrytis blight. This failure is probably due to their inability to penetrate the outer white bulb scale and hence reach the deep-seated mycelium of the causal fungus.

Introduction

Botrytis blight or fire caused by *Botrytis tulipae* constitutes one of the most serious diseases of tulips (6). It is kept under reasonable control in Holland by the use of various measures including foliage sprays (12). Despite these measures, however, many of the bulbs exported to Canada carry the disease. Two hundred and thirty-five interceptions of diseased shipments were made in the London area alone in the years 1948 to 1951 inclusive. Although the average infection was low, between 1 and 2%, a total of 174,576 bulbs were involved in the infected lots. This constitutes an important source of primary infection in greenhouses and gardens.

The present work was undertaken to determine firstly whether a selected group of common fungicides were effective against the causal fungus and secondly whether these fungicides, when applied as bulb treatments, gave any measure of control under greenhouse conditions.

Experiments on the Induction of Sporulation in *Botrytis tulipae* (Lib.) Lind

One of the most widely used methods of assaying fungicides is the slide germination method outlined by the American Phytopathological Society, Committee on the Standardization of Fungicidal Test (1). By this method fungicides are evaluated on the basis of their ability to prevent spore germination. Efforts were therefore made to produce sufficient conidia of *Botrytis tulipae* for this purpose.

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Contribution No. 16, Science Service Laboratory, Canada Department of Agriculture, University of Western Ontario Sub P.O., London, Ontario. Part of a thesis submitted to the University of Western Ontario by the senior author in partial fulfillment of the requirements for an M.Sc. degree.

[2] *Plant Inspector, Plant Protection Division, Science Service, Department of Agriculture, London, Ontario.*

[3] *Principal Plant Pathologist.*

Botrytis tulipae, freshly isolated from a diseased bulb, was cultured on potato dextrose agar, oatmeal agar, and malt agar. These media supported the abundant production of sclerotia but no spores developed. Whetzel's suggestion, referred to by Hopkins (9), of drying out cultures to stimulate conidial production was tried with negative results. An attempt was also made to produce conidia of *Botrytis tulipae* on artificial media by incubating potato dextrose agar cultures of the fungus at 17° C. to determine whether a low temperature would stimulate sporulation as suggested by Newton and Hastings (11). Negative results were again obtained. These observations confirm the statement of Hopkins (9) that *Botrytis tulipae* rarely produces conidia in agar culture under ordinary laboratory conditions, but tends to form sclerotia.

Further attempts to produce sufficient conidia of *Botrytis tulipae* for assay purposes consisted of culturing the organism on natural media. Excised tulip leaves were sterilized with propylene oxide as described by Hansen and Snyder (8), placed in moist chambers, inoculated with a few drops of a mycelial suspension of the fungus, and incubated at room temperature. Observations were made on these cultures daily for 14 days. Only microconidia were observed. A second attempt to produce conidia of the fungus on a natural medium was made by culturing it in moist chambers on freshly excised tulip leaves and petals. Microconidia and macroconidia were produced in eight days on the petals, and in 11 days on the leaves in these cultures. Spore suspensions were made from these cultures. Macroconidia were not, however, present in sufficient numbers to use in the "Slide Germination Method" of assaying fungicides.

The Use of the Thread Method for Testing the Effectiveness of Various Fungicides against Botrytis tulipae

Forsberg (7) described a method of evaluating fungicides by treating pieces of cotton thread infested with *Fusarium oxysporum gladioli*. He immersed the pieces of infested thread in chemical solutions for varying periods of time and then planted them on potato dextrose agar. The results showed a correlation between the size of resultant colonies and both the concentration of fungicide used and the exposure period. The possibility of using this method, with *Botrytis tulipae* as the test organism, was investigated.

Pieces of No. 10 cotton thread, about two inches in length were planted on Petri plate cultures of *Botrytis tulipae*, previously prepared by planting 1 cc. of a mycelial suspension of the fungus in a sterile Petri plate and pouring with potato dextrose agar. The pieces of thread were removed from the culture plates after a suitable incubation period, stripped of excess fungus growth, cut in sections about one-eighth of an inch in length, and collected in sterile Petri plates ready for use.

Aqueous solutions of sodium *o*-phenylphenate were used in a preliminary experiment designed to test the feasibility of using this method. A series of dilutions of the chemical were prepared and pieces of infested thread were

immersed in each for 15, 30, 60, and 120 min. respectively. These pieces of thread were drained on sterile paper immediately following treatment, planted on potato dextrose agar plates, and incubated at room temperature. At the end of three days the diameters of the resultant colonies were measured. It was immediately evident that the relationship between colony size and either length of treatment or chemical concentration was very poor. There did, however, appear to be a reasonable relationship between the concentration of chemical and the number of colonies developing. Accordingly, a second experiment, in which a larger number of pieces of thread were plated, was undertaken in order to test this possibility. In this experiment pieces of thread from 12-day-old cultures of *Botrytis tulipae* were prepared for use in the manner previously described. Numerous sclerotia were present in the cultures at this time. A series of aqueous solutions containing varying amounts of sodium *o*-phenylphenate were prepared in small beakers. Sterile distilled water was included as a control. Thirty pieces of infested thread were placed in each treatment bath and allowed to soak for 30 min. At the end of this period the pieces of thread were removed, drained on sterile filter paper, and planted on potato dextrose agar in Petri dishes at a rate of 10 pieces per plate. Three replications were planted in this way and incubated for two days at room temperature.

The number of pieces of infested thread which failed to produce colonies of *Botrytis tulipae* were counted at the end of the incubation period. The resulting data produced a reasonably fitting straight line when expressed as percentage kill and plotted on probability paper against the logarithm of dosage ($(\text{Chi})^2 = 4.69$; $P(0.05) = 11.1$).

The method was further tested with tetramethylthiuram disulphide (thiram) a relatively water-insoluble substance. The procedure followed was the same as that used in the preceding experiment except that suspensions of the material prepared from a water-wettable commercial product were employed and kept in suspension by agitation during the 30 min. treatment period. The data again produced a reasonably fitting straight line ($(\text{Chi})^2 = 3.31$; $P(0.05 = 7.82)$.

It was concluded from this work that the thread method as modified for use in these tests was satisfactory for the laboratory evaluation of the effectiveness of fungicides against *Botrytis tulipae*.

The Toxicity of Miscellaneous Fungicides to Botrytis tulipae

The thread method, as described in the preceding section, was used to test the *in vitro* effectiveness of a number of fungicides against *Botrytis tulipae*. The fungicides tested and the reasons for their selection were as follows:—

1. Sodium *o*-phenylphenate (Dowicide A)—recently reported (2, 3) to give effective control of several pathogens of orchids and tuberoses in established lesions without causing host injury.

2. Thiram—(tetramethylthiurum disulphide) (Thiuram SL)—recommended as a postemergence spray for the control of *B. tulipae* in Holland and other parts of Europe (12, 13).

3. Ferbam—(ferric dimethyldithiocarbamate) (Fermate)—recommended as a postemergence spray for the control of *B. tulipae* in Washington State and in Holland (14, 12).

4. Chloranil—(Tetrachloro-*p*-benzoquinone) (Spergon)—recommended as a gladiolus corm treatment for the control of several diseases, including *Botrytis* neck rot (4).

5. A mixture of the sodium salts of dimethyldithiocarbamic acid and 2-mercaptobenzothiazole (Vancide 51) was included because of the manufacturer's claims of systemic activity.

The results obtained are summarized in Fig. 1.

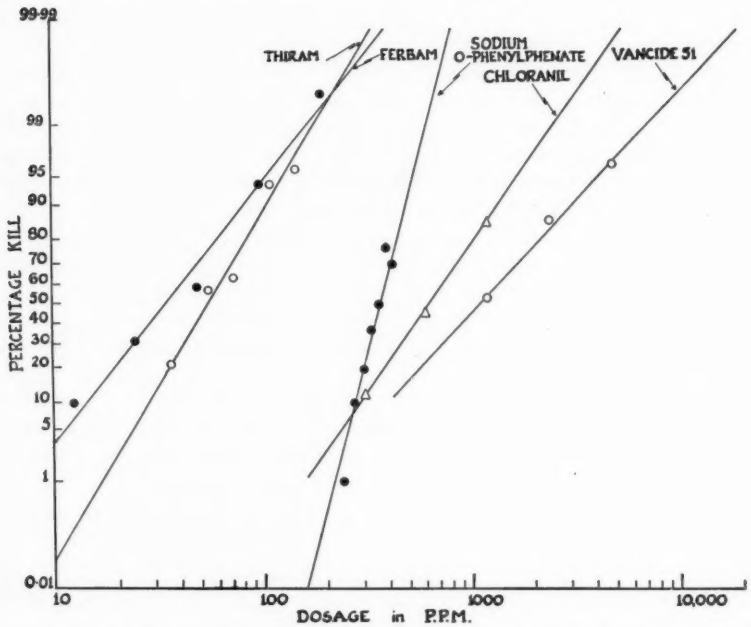

FIG. 1. An *in vitro* comparison of the effectiveness of certain fungicides against *Botrytis tulipae*.

Thiram and ferbam are each effective against *Botrytis tulipae* at lower concentrations than either chloranil or Vancide 51. Sodium *o*-phenylphenate is intermediate at the LD_{95} point but its probit log concentration regression line is of steeper slope than those of thiram, ferbam, or chloranil which are parallel. This parallelism is a good indication that these compounds have a similar mechanism of action. Similarity of action of thiram and ferbam was noted by Barratt and Horsfall (5). Evidence for it was also obtained by Klöpping (10) who showed that the range of effectiveness of these compounds, against

FIG. 2. Bulb and plant symptoms resulting from infection by *Botrytis tulipae*.
Upper: A group of the most severely infected bulbs used in the bulb treatment studies.
Lower: General appearance of plants and forced bulbs, regardless of preliminary bulb treatment.

various fungi, coincided. The similarity of action between these two compounds is perhaps a reflection of their close chemical relationship. Such an explanation would not, however, readily account for the parallelism between the regression lines for chloranil and thiram. Here the similarity of action may result from some physical factor, such as ability to penetrate, rather than molecular structure.

Bulb Treatment for Blight Control

Darwin tulips of the City of Haarlem variety showing a high percentage of infection by *Botrytis tulipae* were used. The bulbs were divided into 14 lots of approximately 14 bulbs each. These lots were selected as carefully as possible to ensure an equal disease incidence in each. All treatments were applied as dips in either solutions or slurries.

The concentrations and lengths of dip used for the various treatments were as follows: sodium *o*-phenylphenate (Dowicide A), 0.05%, three hours and six hours; thiram 12.5%, three minutes; ferbam (Fermate), 0.5% two minutes; chloranil (Spergon), 0.8%, two minutes; and Vancide 51, 2.0%, five minutes. These rates of treatment were arrived at by consulting the literature rather than from the results reported in the preceding section since the laboratory work was conducted while this experiment was in progress. The treatments were applied to duplicate lots of bulbs. The bulbs were planted in six-inch flower pots, held at a temperature of approximately 52° F. for eight weeks, transferred to a greenhouse and maintained under night temperature conditions of approximately 55° F. for two weeks, and finally placed under warmer conditions for flowering.

Observations were made on the plants throughout their growth period. Abundant disease development occurred, as illustrated in Fig. 2 but no differences between treatments were apparent. At maturity the bulbs were washed free of soil and examined for disease. Again, no differences were observed. None of the treatments used caused any observable bulb or plant injury.

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EFFECTS OF EXPOSURE TO DIRECT SUNLIGHT UPON THE DEVELOPMENT OF LEAF STRUCTURE OF TWO DECIDUOUS SHRUB SPECIES[1]

By R. G. H. Cormack[2] and Anne L. Gorham[3]

Abstract

The present anatomical study of sun and shade leaves of two shrub species *Menziesia glabella* and *Lonicera glaucescens* is an outgrowth of interest in the response of ground cover plants to increased sunlight as the result of logging operations. Leaves of both shrub species developed on plants fully exposed to the sun are smaller, thicker, more compact, with longer palisade cells, less spongy mesophyll, and thicker cuticle than comparable leaves from plants growing normally in deep shade. Evidence is given for the views that (1) differences in leaf expression are not predetermined by the environment of the bud during its formation the previous season, and (2) structural modifications that result when typical shade buds are suddenly exposed to full sunlight are merely an indication of the plasticity of leaves to light.

Introduction

A previous paper (2) describes the effects of heavy indiscriminate cutting upon the ground vegetation of a virgin spruce woods in the mountainous southwest corner of Alberta. The most striking effect produced by the removal of the tall spruce is the drying out and subsequent death of the shade-loving plants. The unusual foliar appearance of certain shade-loving shrubs struggling for existence in the changed environment suggested that this location might yield interesting leaf material for a comparative anatomical study. Consequently while making another forest survey in the same area during the summer of 1952, collections were made of the leaves of two mountain shrubs, *Menziesia glabella* A. Gray and *Lonicera glaucescens* Rydb. These two shrubs stand out most clearly as indicating the moist cool environment of virgin spruce woods (3), and are among the first to perish from exposure on the removal of the tall trees.

The study of environmental factors and their effects upon developing plant organs and tissues is of major importance in botanical research. It is well known that the leaves of higher plants are very sensitive to light; in general, high light intensity produces thick, well-differentiated leaves (sun leaves), while those produced in the shade (shade leaves) are thin and poorly differentiated. Lundegårdh (6) classified the higher plants into three categories: (1) extreme sun plants which form only "sun leaves", (2) extreme shade plants which form only "shade leaves", and (3) plants which flourish in both sun and shade and are able to form both types of leaves. Although the terms sun and shade leaves are of common usage, only a few workers following Lundegårdh have specified whether the plants under investigation were normally sun plants or shade plants.

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Most of the anatomical investigations have dealt with mature leaves almost exclusively and little attention has been paid to modifications in leaf structure induced by a sudden change in light intensity just prior to the opening of the buds. The only investigations approximating a study of this kind which have come to the authors' attention are the experiments of Isanogle (5) and Watson (9). The former experimented with the opposite buds of the twigs of *Cornus florida rubra* André and *Acer platanoides* L. by shading one bud, leaving the other of the experimental pair to develop normally. Watson investigated the effects of controlled environment on both mature and developing leaves of the English ivy, *Hedera helix* L.

Materials and Methods

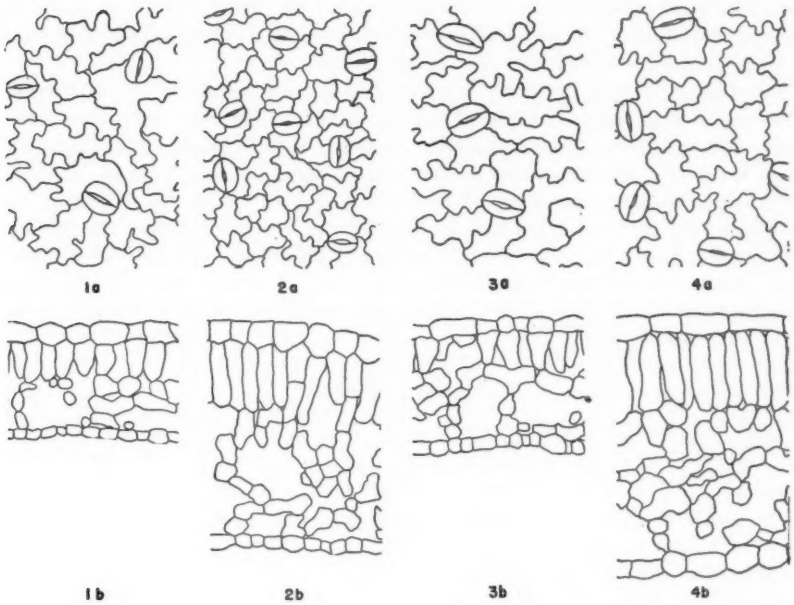
Leaves, herein designated as sun leaves, were collected from plants growing in an area heavily cut over the previous winter and now fully exposed to direct sunlight and to strong drying winds. Leaves obtained from plants growing normally in the deep shade of adjacent undisturbed areas are designated as shade leaves and serve as controls in the present study. The sun leaves had developed from buds produced in deep shade the previous year, but had expanded and reached maturity in direct sunlight. They were strikingly smaller, thicker, and much paler in color than shade leaves. Not only were they thicker but they also had a stiff unnatural appearance and felt leathery to the touch.

Since the collection date was Aug. 20, 1952, all the leaves were considered to have reached their full development for the season. *Menziesia* shade leaves measured 5.5 to 6.5 cm. long and 2.5 to 3 cm. wide and sun leaves 2 to 3 cm. long and 1 to 1.5 cm. wide. *Lonicera* shade leaves were 7 to 9 cm. long and 4 to 5 cm. wide and sun leaves 4 to 5.5 cm. long and 3 to 4.5 cm. wide.

Typical leaves were removed from both exposed and shaded plants at approximately the same distance from the ground and killed in FAA. At a later date small rectangles from these leaves were dehydrated in normal butyl alcohol, embedded in paraffin, and cut transversely at a thickness of 10 microns. The sections were stained with Delafield's haematoxylin and safranin and then mounted in Canada balsam. In addition, epidermal peels were prepared from the same material.

Results

From the illustrations (Figs. 1–4) and from measurements in Table I the differences between shade and sun leaves are easily recognized. Sun leaves of both shrub species are thicker, more compact, with longer palisade cells, less porous spongy mesophyll, and appreciably thicker cuticle particularly on the upper surface. Internally the difference in leaf thickness is brought about by a combination of additional cell rows and increased cell enlargement in the mesophyll. For instance, in *Lonicera* where the difference in leaf thickness is especially striking, the shade leaves have regularly five to six layers of cells of which two or three are sponge tissue. The sun leaves have seven to nine



FIGS. 1*a*, 1*b*, 2*a*, and 2*b*. Lower epidermis and cross sections of comparable *Menziesia glabella* leaves, ×165: Figs 1*a* and 1*b*, leaf from plant growing normally in deep shade with enlarged lower epidermal cells and thin cross section; Figs. 2*a* and 2*b*, leaf from plant exposed to direct sunlight, with much smaller lower epidermal cells, much thicker cross section, and greater number of cell layers as in the shade leaf in Figs. 1*a* and 1*b*.

FIGS. 3*a*, 3*b*, 4*a*, and 4*b*. Lower epidermis and cross section of comparable *Lonicera glaucescens* leaves ×165: Figs. 3*a* and 3*b*, leaf from plant growing normally in deep shade with enlarged lower epidermal cells and thin cross section; Figs. 4*a* and 4*b*, leaf from plant exposed to direct sunlight with much smaller lower epidermal cells, very much thicker cross section, and greater number of cell layers as in the shade leaf in Figs. 3*a* and 3*b*.

TABLE I

MEAN THICKNESS IN MICRONS OF UPPER AND LOWER EPIDERMIS, PALISADE AND SPONGY TISSUES, AND TOTAL LEAF THICKNESS OF SUN AND SHADE LEAVES OF *Menziesia* AND *Lonicera*

Species and type of leaf	Upper epidermis	Palisade tissue	Sponge tissue	Lower epidermis	Total leaf thickness
Menziesia					
Shade leaf	16.3	37.8	52.5	10.3	117
Sun leaf	21.3	61.5	84.2	10.7	178
Lonicera					
Shade leaf	16.5	36.3	51.8	12.0	117
Sun leaf	21.2	79.5	117.1	18.1	236

layers, four to six of which are sponge tissue. Typically there is one row of palisade cells in both shade and sun leaves but in the latter it is modified in places particularly in the neighborhood of the larger veins. This condition is much the same for *Menziesia*.

The areas of sun leaves are considerably less than those of shade leaves. In comparing total leaf areas of mature leaves, *Menziesia* sun leaves have only 15 to 25% and *Lonicera* sun leaves 30 to 50% of the area of comparable shade leaves. Accompanying the decrease in leaf area there is also a decrease in surface areas of individual cells of both upper and lower epidermis. This is not fully apparent in cross section. But, lower epidermal peels (Figs. 1*a*–4*a*) show that there are many more cells per unit area (area of high power field) of sun leaves than in shaded ones. Similarly it may be seen that the stomata which occur only on the lower surface are twice as numerous per unit area in sun leaves as in shade leaves.

Discussion

Since the literature on light and shade leaves has been ably reviewed by Burkholder (1), Isanogle (5), and Shields (8), it is necessary only to discuss those aspects which are pertinent to the problem in hand.

Leaves described as sun leaves in the present paper are not to be confused with leaves from plants which grow normally in the sun (5, 7, 9), nor with exposed leaves in the crown of an isolated tree (4, 10). In the present paper the term sun leaves refers to leaves that developed in direct sunlight from buds produced the year before in deep shade, on plants which must be considered as extreme shade plants. A comparable study is that of Isanogle (5), with this difference that the plants she worked with, namely, *Cornus florida rubra* and *Acer platanoides*, normally form both sun and shade leaves while those in the present study are definitely shade plants. For this reason it is interesting to compare her observations with those of the present study.

In her experiments, one of a pair of opposite buds at the same node was shaded while the other was exposed to full sunlight. The exposed bud served as a control. Her observation that exposed leaves are thicker than shaded leaves agrees with the present study. In her plants the greater thickness of exposed leaves was due to cell enlargement only, while in *Lonicera* and *Menziesia* it was due to additional cell rows as well as to cell enlargement.

Also, in the plants studied by Isanogle, mature shade leaves were smaller and possessed many more epidermal cells in a given area than comparable unshaded ones. In *Lonicera* and *Menziesia*, on the other hand, the sun leaves were smaller and carried many more epidermal cells in a given area than normal shade leaves.

In regard to differences in size between sun and shade leaves Watson's experiments (9) with English ivy are of interest. He concluded that marked differences in leaf size result when plants are moved so that they are no longer in equilibrium with their environment. Plants removed in summer from a

comparatively humid atmosphere to brighter and drier conditions developed very small leaves, while sun plants transferred to dark shade conditions developed exceedingly large leaves.

Penfound (7), Watson (9), and others have found that available moisture is a causative factor for structural differences between sun and shade leaves. This does not seem to be the case in the present study. The growing season of 1952 for this mountainous region was one of almost continuous rain. At the time the leaves were collected the thick moss carpet and surface soil was saturated with water. Hence, all differences between leaves from exposed plants and those from plants growing normally in the shade result solely from responses to increased light intensity.

These observations confirm the conclusion of Isanogle that differences in leaf expression are not predetermined by the environment of the bud during its formation the previous season. The so-called xeromorphic characters, namely thicker cuticle, rather closely packed palisade and sponge tissue, that result when the buds are suddenly exposed to direct sunlight are merely an indication of the plasticity of leaves to this factor (6). That these modifications have no survival value in themselves (8) seems evident from the observation that in areas cut over two years or more, all the shade-loving shrubs are dead.

Acknowledgment

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SURVIVAL AND PATHOGENICITY OF *ALTERNARIA RAPHANI* AFTER FIVE YEARS IN DRIED SOIL CULTURES[1]

By R. G. Atkinson[2]

Abstract

Soil cultures of *Alternaria raphani*, a seed-borne pathogen of radish, that had become dry when four to six weeks old, were still viable after five years. The incidence of residual viable centers in cultures of four of the five wild types studied was much higher than in those of their respective variants, on the basis of colony counts from platings of 5-gm. samples diluted one-fifth. The reverse of this was true for the remaining wild type and its variant. This pair was also unique in that the wild type had been shown to possess little infectivity, whereas its variant had proved to be highly virulent. The fungus showed no change in cultural characteristics after its five-year period in dry soil, nor any loss of virulence when plants of radish, stock, and wallflower were inoculated.

Introduction

The usual method of maintaining cultures of microorganisms on agar slants by subculturing them periodically has many obvious disadvantages. In an attempt to overcome these, Sherf (10) developed the oil method in which a layer of sterilized mineral oil completely covers the agar and mycelium of slant cultures. Buell and Weston (2) have reported that oil-treated cultures of fungi from a wide taxonomic range remained viable for test periods of from 12 to 24 months.

Unfortunately, however, only meager information is available concerning the pathogenicity of fungi kept under these conditions. Wernham and Miller (11) stated that cultures of *Diplodia* sp., *Gibberella* sp., and *Helminthosporium maydis* Nisik. & Mke. "appeared to be actively pathogenic after three years under oil".

The use of sterilized soil for the culture of microorganisms is probably a common practice in many laboratories but there appears to be little information in the literature indicating the groups and species that can best survive in this substrate. Greene and Fred (5) found that *Aspergillus fischeri*, *A. sydowi*, and *Penicillium chrysogenum* survived in dried soil cultures for over two years without loss of their desirable fermentation capacities, or their typical colony characteristics. Miller (8) found that tubes of moist sterilized soil inoculated with the muskmelon wilt *Fusarium*, and allowed to dry out, provided a ready and convenient source of inoculum. When tested after three years, the fungus showed no change in cultural characteristics nor any loss of virulence. Fennel *et al.* (4), working with mucoraceous fungi, found that next to lyophilization the dried soil culture technique was most efficient in maintaining viability. Jones (6) maintained certain saprophytic actinomycetes for four and a half years in cultures of moist sterilized soil, and when these were plated on a synthetic agar medium they showed "the color,

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sporulation, and enzymatic behavior which characterized the original isolates from nature". Erikson (3), on the other hand, successfully maintained several strains of actinomycetes for periods of more than one year in sterile soil that was allowed to become dry. He also found that when these soil cultures were plated on a synthetic agar medium, all strains had retained the development of normal aerial mycelium. When the same strains were grown in nutrient glucose broth, however, and then similarly plated, variant sectors or colonies devoid of aerial growth appeared.

In connection with previous studies on *Alternaria raphani* Groves and Skolko, a seed-borne pathogen of radish (1), the writer found that certain wild type strains of this fungus, and their cultural variants, had survived 18 months in dried soil cultures with no loss of pathogenicity or change in cultural characteristics.

Recently, the viability and pathogenicity of these soil cultures have been tested after a period of more than five years. The positive nature of the results seemed to be sufficiently striking to bring them to the attention of others, especially in view of the almost complete lack of information in the literature concerning the fungi that might be successfully maintained over long periods by means of the relatively simple soil culture method.

Materials and Methods

The strains of *A. raphani* under investigation comprised five wild types isolated from diseased radish in the field and their five respective variants that arose from them in potato-dextrose-agar cultures. Duplicate soil cultures of each strain had been prepared by transferring pieces of mycelium and agar from monosporous colonies to tubes of moistened, sterilized loam soil. Both sets of cultures, one initiated in March, 1947 (Series I) and the other in June, 1947 (Series II), were kept at room temperature on a shelf in diffused light. They dried out in four to six weeks and no water has been added to them since.

On May 30, 1952, after more than five years, samples of the dry soil cultures were plated to determine whether *A. raphani* could survive such an extended period of desiccation. To gain some idea of the adaptability of each strain for survival under these conditions, the dilution plate technique was employed to estimate the numbers of viable centers remaining in each culture. On the basis of a preliminary plating of one of the soil cultures, dilutions of 1/5, 1/10, and 1/20 were chosen for these tests.

Five grams of soil from the upper portion of each culture, or about one-fifth of the total, was suspended in 25 cc. of sterile water, making a dilution of 1/5. This exceedingly heavy suspension was shaken for five minutes and serial dilutions, each having a final volume of 20 cc., were prepared and agitated for two minutes. For each of the cultures tested, 1-cc. aliquots of the three dilutions were plated, the 1/5 in triplicate and the others in duplicate. The aliquots were pipetted from the dilutions immediately after being vigorously shaken and, although the soil settled rapidly, a considerable quantity was

present in the portions withdrawn and plated. The plating medium was potato dextrose agar supplemented with oxgall[3] at the rate of 2%. This procedure was repeated with second 5-gm. samples from certain of the soil cultures. Oxgall inhibits the growth of bacteria and actinomycetes (7), but was used here because in agar culture it also restricts the spreading of fungous colonies, thereby permitting more accurate plate counts when estimating populations of these organisms. Miller (9) found that the average numbers of fungous colonies that developed from soil dilutions plated on potato dextrose agar with, and without, oxgall were essentially similar. Colonies on the plates were counted after five days' incubation at 27° C.

To provide inoculum for testing their pathogenicity, the wild type strains from the plated dilutions were grown on potato dextrose agar supplemented with yeast extract. The presence of the latter material had been shown previously (1) to stimulate sporulation in *A. raphani*.

Spore and hyphal suspensions from the above cultures were then atomized on three-week-old radish and eight-week-old stocks and wallflowers, the three hosts used in the earlier study of *A. raphani* (1). The inoculated plants were kept for four days in moist chambers with a relative humidity close to 100% and a temperature varying from 24° to 30° C.

Results and Discussion

Viability of the Soil Cultures

Wilt Type Strains

Viable inoculum of each of the five wild type strains was still present in the soil cultures in both series, despite their desiccated condition of approximately five years' duration. The number of colonies appearing in the dilution plates is presented in Table I. These values show considerable variation among replicate plates and also between duplicate samplings of certain of the soil cultures. The replicate variations may have been due to a very close association of viable inoculum with the soil grains and to the difficulty of pipetting aliquots containing similar quantities of grains from such heavy suspensions in which most of the soil soon settled. The discrepancy between plate counts from duplicate samplings may have resulted from the occurrence of varying proportions of viable inoculum in different parts of a given soil culture.

Despite these variations, however, the data in Table I appear to establish certain trends. The plate counts from the cultures of strains I-S1, I-S2, and IV-S4A in series I were considerably lower than those of the same strains in series II. These results may merely reflect fortuitous variations in sampling. On the other hand, the number of viable centers in the cultures of these strains may have dropped sharply after five years, thereby accounting for the lower number of colonies obtained from them in series I, which was approximately five years and three months old when sampled. The extremely low

[3] *Bacto-Oxgall, prepared by Difco Laboratories.*

TABLE I

NUMBER OF COLONIES IN PLATED DILUTIONS OF FIVE YEAR OLD, DRIED SOIL CULTURES OF FIVE WILD TYPE STRAINS OF *A. raphani*

Strain	Dil.	Soil culture series I					Soil culture series II				
		Replicate plates			Av.	Viable centers/ gm. soil	Replicate plates			Av.	Viable centers/ gm. soil
		1	2	3			1	2	3		
I–S1	1/5	2	4	0	2††	10	26	39	12	25.6	128
	1/10	1	0	—			3	0	—		
	1/20	2	0	—			0	0	—		
I–S2	1/5	3	11	5	6.3	31.5	†(*a*) 10	41	14	21.6	108
							(*b*) 249*	194*	222*	221.6	1108
	1/10	2	1	—			3	6	—		
	1/20	0	0	—			1	0	—		
IV–S4A	1/5	(*a*) 56	34	5	31.6	158	(*a*) 17	6	38	17	85
		(*b*) 33	11	12	18.6	93	(*b*) 220*	89	110	139.6	698
	1/10	1	4	—			3	6	—		
	1/20	2	1				1	0	—		
III–S4C	1/5	(*a*) 40	68	56	54.6	273	(*a*) 14	12	1	9	45
		(*b*) 26	23	15	21.3	106.5	(*b*) 126	55	16	65.6	328
	1/10	1	4	—			3	6	—		
	1/20	2	1	—			1	0			
II–S6	1/5	21	14	12	15.6	78	30	24	11	21.6	108
	1/10	5	1	—			1	1	—		
	1/20	2	1	—			1	0	—		

* *Plates very crowded, counts only approximate.*

† *Results from duplicate samples of cultures, the values for dilutions of 1/10 and 1/20 are from the same sample as those in (a).*

†† *Based on plate counts from dilution of 1/5.*

counts of viable centers in culture I-S1, in series I, may or may not be related to the lack of virulence in this strain (1). Evidence against any such relationship is the fact that, although the plate counts of this strain in series II are also low, those of II-S6 are somewhat lower, despite the fact that the latter strain was shown to be highly virulent.

Variant Strains

Plate counts of the soil cultures of the variant strains appear in Table II and, except for those of I-S1, they are strikingly lower than the corresponding values of the respective wild types from which they arose. In fact, the highest count from the soil culture of variant IV-S4A was only 14 and from that of I-S2 only 2. No colonies developed in the dilution plates of III-S4C and IIS-6. Some viable inoculum was still present in the soil cultures of these two variants, however, because when an excess of soil grains from them was scattered over agar slants a few colonies did appear.

TABLE II

NUMBER OF COLONIES IN PLATED DILUTIONS OF FIVE YEAR OLD, DRIED SOIL CULTURES OF FIVE VARIANT STRAINS OF *A. raphani*

Strain	Dil.	Soil culture series I					Soil culture series II				
		Replicate plates			Av.	Viable centers/ gm. soil	Replicate plates			Av.	Viable centers/ gm. soil
		1	2	3			1	2	3		
I–S1*	1/5						161	96	72	109.7	548.5
	1/10						22	20	—		
	1/20						7	4	—		
I–S2	1/5	1	0	0	0.33	1.6	1	1	0	0.7	3.5
	1/10	0	0	—			0	0	—		
	1/20	0	0	—			0	0	—		
IV–S4A	1/5	1	9	13	7.7	38.5	14	1	1	5.3	26.5
	1/10	7	0	—			2	0	—		
	1/20	0	0	—			0	0	—		

* *The soil culture of variant I-S1 in series I had been shown to be nonviable after 18 months (1). No colonies appeared in any of the plated dilutions from the soil cultures of variants III-S4C and II-S6.*

The plate count of the variant I-S1 was by far the highest and, with two exceptions, was greater than any from the wild type cultures. The only other cultures among the variants that showed appreciable numbers of viable centers were those of IV-S4A. It is interesting to note that both of these variants were previously shown (1) to be as pathogenic as the wild types and that they also develop abundant pigmentation in their mycelia. In contrast, the remaining variants, I-S2, III-S4C, and II-S6 which showed poor survival in the soil cultures, also possess a low order of virulence and develop little or no pigmentation.

The survival of *A. raphani* in the dry soil cultures for such a long period is probably related to the formation of thick-walled chlamydospores in this species, and possibly to the presence of dark pigmentation in these bodies and in the vegetative hyphae and conidia. In this connection, the only variant that showed the same capacity as the wild types to survive in the dried soil cultures, i.e. I-S1, is also the only one that forms chlamydospores (1).

The colonies that developed from the dilutions of the soil cultures of the wild type strains showed no loss of their typical cultural characteristics, such as pigmentation, aerial habit, chlamydospore formation, and sporulation. Evidently the wild types remained stable over the five-year period in the dry soil cultures. This was also true of the cultures of the variants.

Pathogenicity Tests

The results of the pathogenicity tests of the wild type strains recovered from the soil cultures are given in Table III.

TABLE III

VIRULENCE OF FIVE WILD TYPE STRAINS OF *A. raphani* AFTER FIVE YEARS IN DRIED SOIL CULTURES

Strain	Radish	Stock	Wallflower
I-S1	+	+	+
I-S2	++++ $\frac{3}{4}$*	++++	+++
IV-S4A	++++ $\frac{4}{4}$	++++	++++
III-S4C	++	+++	++
II-S6	++++ $\frac{3}{4}$	++++	++++

+ = trace of infection, few, discrete, small lesions; ++ = slight infection, larger lesions; +++ = moderate infection, some coalescence of lesions, slight yellowing of leaves; ++++ = plants dead or severely infected, leaves withered.

* *(plants killed)/(plants inoculated).*

The results showed that all of the wild type strains were as virulent after five years in the dried soil cultures as they were soon after their original isolation from the field (1). It is clear, then, that the soil culture method provides an excellent means of preserving the pathogenicity of *A. raphani* for long periods.

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FURTHER STUDIES OF BIRCH DIEBACK IN NOVA SCOTIA[1]

By K. N. H. Greenidge[2]

Abstract

Well-marked differences, involving both the patterns of moisture movement and storage, have been found to separate the water relationships of yellow birch, *Betula lutea* Michx., in various stages of deterioration. The cumulative results of injection studies, root excavations, and an extended survey of the trends in moisture distribution in the species over a prolonged period, suggest that the locus of action of the disease is, in the first instance, in the roots, and that excessive rootlet mortalities in apparently healthy trees constitute the initial indication of a diseased condition in the species.

Introduction

Investigations into the cause of the widespread injury to native species of birch in northeastern North America were initiated in Nova Scotia in 1944. The results obtained during the initial phases of this study suggested that the decline of the species was most logically to be attributed to the interaction of numerous environmental, metabolic, and morphological considerations (4, 5), and projects commenced subsequent to 1948 were designed with a view to clarifying the relative significance of these several variables. The investigation of various aspects of the moisture economy of yellow birch, *Betula lutea* Michx., constituted an integral part of these studies. Material selected for investigation embraced a wide range of injury conditions, and the salient features of the results of these studies are outlined in the following paragraphs. In the present paper the crown injury classification proposed by Hawboldt and Skolko (5) has been adopted with minor modifications: for ease of reference the suggestions advanced by these investigators are outlined below.

Crown Injury Classification of Birch

Class	Foliage Description
1A	Normal tree. Foliage full size and rich in color. No dead twigs or branches.
1B	As in 1A, except for presence of dead twigs or branches as may be attributed to suppression, whipping, logging, or other mechanical injury.
2A	Foliage abnormally small, curled, thin, yellowish, or otherwise weak in appearance, but not conspicuously so. (This may be a seasonal condition and not represent true dieback; the tree may appear normal the following year). No dead twigs or branches, except as in 1B.
2B	As 2A, but decidedly and conspicuously so.
(3A)	A normal tree, except that it has a number of dead, that is bare twigs, in the top of the crown other than as in 1B, such bare twigs perhaps being in a moribund state, and hence representing one of the early symptoms of dieback.

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3A Trees with apparently dead twigs (may be living but bare) for no obvious reason, but no dead branches. Such twigs occurring at the ends of the branches, usually in the top of the crown. In this and subsequent categories the foliage is usually, but not necessarily weak.

3B Trees with dead branches for no apparent reason, but such branches to constitute less than half the crown. A "branch" should be at least 3 or 4 ft. long and there should be two or three dead before the tree is placed in this class.

4A Trees with over half the crown dead.

4B As 4A, but no living branches except small adventitious ones, usually to be found at the base of the crown.

5A Crown dead but cambium green at breast height.

5B As 5A, but cambium dry at breast height. Tree recently dead, that is with most of the fine twigs still adhering.

6A Tree dead for several years. Most of the smaller twigs gone.

6B As 6A, but only the stem and primary branches remaining.

Materials and Methods

A preliminary survey of the water economy of healthy and diseased yellow birch was commenced in 1949 with a reconnaissance of the patterns of moisture movement and retention in trees of all crown injury classes. This preliminary study was followed in 1950 and 1951 by a critical consideration of the distribution and utilization of moisture in the species over a period of 14 months.

The patterns of moisture movement in the species were investigated by means of the injection of water-soluble dyes into the lower boles of trees of all injury classes from 1A to 4B inclusive. The pan and chisel-cut method of Banfield (1) was employed in principle throughout. A 0.25% solution of acid fuchsin was found by experiment to give an adequate staining pattern, and this concentration was used during the entire 1949 and 1950 seasons. To trace the over-all patterns of conduction in the individual tree, the entire circumference of the bole at breast height was incised, below the surface of the dye solution, to a depth of 0.75-1.00 in., and the tree left to take up the solution for a varying period. Following treatment each tree was felled, peeled, and cut into bolts of requisite length, and the distribution patterns traced from roots to apex in longitudinal and transverse section. A total of 77 trees was investigated in this phase of the study.

The distribution of moisture in healthy and diseased material was investigated in the interval 1949-1951 using the technique of Craib (2) as modified by Gibbs (3). Complete transverse discs were taken from the butts, upper boles, and crowns (butts, middles, and tops respectively in Table II) of trees of all crown injury classes from 1A to 4B inclusive. Strips were then removed from the discs and divided into nine sample blocks. The size of each sample was so regulated that Blocks 1 and 9 constituted the outer sapwood, 2, 3, 7, and 8 the inner sapwood, and 5 the heartwood. Samples were weighed

immediately, dried at 105° C. for 48 hr., cooled in a desiccator, reweighed, and the moisture content determined on a dry weight basis. In this phase of the investigation 167 trees were felled and analyzed.

In view of the close relationship between rootlet condition and the over-all moisture economy of trees, excavation studies of the root systems of yellow birch which were initiated in 1947 were continued throughout the growing seasons of 1948 and 1950. A Bickle Seagrave "150" pump developing 25 horse power and delivering upwards of 150 gal. of water per minute was employed to cut and clear away the soil surrounding the root systems of the experimental trees. The pressure at the pump was so regulated that the pressure at the nozzles remained constant at 15 lb. per sq. in. Two hose lines were led away from the pump, and at a convenient distance from the machine Y-connectors were inserted into the system. In this manner four streams of water were brought into action at the excavation site. Initially two of the hoses were fitted with 0.5 in. nozzles and used for cutting while the other two lines remained open and were used for sluicing. Later, however, all four lines were equipped with nozzles. This alternative technique proved to be much more effective and was used to great advantage during the greater part of the 1950 season.

Following excavation, the exposed root system of each tree was marked off in four quadrants, and from each of these sectors a very large sample of feeding rootlets was collected. Rootlet mortality for each sector was determined on the basis of a count made of 500 rootlets selected at random from the sample collected from the given quadrant. Percentage rootlet mortality for the entire tree was then derived from the counts of the individual sectors.

Observations and Results

A large body of information was accumulated during the course of the present study dealing with various aspects of the movement and storage of moisture in yellow birch. For reasons of conciseness, only those aspects of these processes which are directly concerned with the disease will be considered in subsequent paragraphs. Seasonal trends and variations in the patterns of moisture distribution will be reviewed only for the period of active growth in Nova Scotia, i.e. June to August inclusive. Similarly, the patterns of moisture movement will be considered only in so far as they amplify the moisture distribution picture, or contribute in some other manner to an understanding of the immediate problem of birch dieback.

1. Injection Studies

The descriptions included below of the staining patterns noted in trees in various stages of deterioration are based upon the results obtained from a total of approximately 80 trees. Summarized data illustrating the general characteristics of sample material together with the results obtained in randomly selected trees of each injury class are presented in Table I.

TABLE I

DISTRIBUTION OF WATER-SOLUBLE DYES IN HEALTHY AND DISEASED YELLOW BIRCH

Tree No.	Injury class	D.B.H. (in.)	Height (ft.)	Injection time (hr.)	Amount absorbed (liters)	Height of staining (ft.)
49-28	1A	5	50	47.0	6.8	50
49-29	1A	4	36	50.0	4.9	36
49-15	1B	5	53	27.3	18.5	53
49-39	1B	5	43	114.0	4.8	43
49-6	2A	7	55	44.7	4.0	55
50-13	2A	6	46	22.0	7.5	46
50-1	2B	6	38	4.3	9.8	38
50-367	2B	6	44	—	7.0	44
49-9	3A	8	55	21.6	10.0	55
49-11	3A	10	63	24.2	20.0	40
49-17	3A	12	65	48.0	28.0	65
49-18	3A	7	55	93.4	16.8	55
49-19	3A	5	50	93.0	5.0	50
49-37	3A	7	61	75.0	20.8	61
49-14	3B	7	59	24.3	2.5	28
49-20	3B	9	60	76.8	8.8	47
49-26	3B	11	56	70.3	15.0	29
49-34	3B	7	59	70.9	10.0	40
49-36	3B	12	62	142.8	12.0	26
49-40	3B	8	62	75.2	11.5	25
49-12	4A	12	64	51.5	9.0	25
49-16	4A	6	46	93.0	3.0	23
49-24	4A	7	62	96.8	6.0	13
50-5	4B	6	51	22.5	0.6	13
50-6	4B	9	54	22.0	4.5	8
50-18	4B	6	40	—	0.8	3

In trees of injury classes 1A–2B inclusive the dye solution moved vertically upwards, and downwards, in the outer growth layers, reaching the terminals readily. Thus in longitudinal surface view, a continuous staining pattern was evident in trees with bark removed. The injection fluid, in addition to moving vertically upwards, also moved radially inwards a variable distance, frequently to the outer limits of the heartwood. Thus the entire cross section of the sapwood appeared capable of functioning in water conduction. This marked radial transfer took place over a variable vertical extent, the pattern being maintained as the dye solution moved into the crown. Conduction rates in injected trees varied widely, and were correlated with such factors as time of day, wind velocity, cloud cover, relative humidity, size of tree, crown class, foliar surface, and possibly other factors. In healthy trees, from 15 to 60 ft. in height, the cone frustrums remained in position from 1 to 77 hr., the uptake of dye solution ranging from 4 to 20 liters.

Marked deviations from the above patterns of staining were evident in slightly to moderately diseased material (class 3A and 3B trees). These differences became apparent at variable, but moderately short distances above the injection level. The dye solution rose a limited distance in the outer rings of diseased trees (3-25 ft.). Owing to inequalities in the height to which the injection fluid travelled on different radii, an irregular streaking in the outer sapwood was very evident. The upper limit of this streaking marked the level at which the dye solution ceased to move in the outer growth rings. Above this level, staining was not apparent in transverse sections of the youngest growth layers, although it was very evident in the inner sapwood. The width of the dyed region decreased radially with increased height, paralleling the decrease in the amount of dye solution moving in the outer growth layers. Thus in cross sections of the bole there could be observed a ring of stained wood of varying radial width, the outer limit of which was displaced 0.5-0.75 in. inward from the outer edge of the sapwood.

The dye solution reached the apex in the majority of injected class 3A trees, although the staining patterns observed in the crowns of these trees were, in contrast to those of healthier classes, very irregular and discontinuous. The leaves of a given twig showed much variation in the intensity of staining. Some leaves apparently took up no solution, others appeared to be functioning normally, and thus a very uneven staining pattern was commonly to be observed. In class 3B trees, however, the injection medium commonly moved into the foliage of the lower crown, but failed in every case to reach the upper terminals. Following injection, a number of class 3B trees showed a region of intense coloration to a distance of approximately 18 in. above and below the incision. This region of very heavy staining was never extensive, and its continuity was quickly disturbed by the streaking pattern whose development has been described above. Slightly to moderately diseased material selected for study ranged from 36 to 65 ft. in height with injection periods varying from 1 to 143 hr. The deviations from normality noted in the conduction patterns of class 3A and 3B trees did not appear to be correlated with date of injection subsequent to the onset of active transpiration in the species. Similar patterns of staining were to be observed in June, July, and August, the degree of divergence from normal apparently constituting a characteristic of the individual tree.

The staining patterns observed in heavily diseased material (class 4A and 4B trees) differed further from those described above. These trees were likewise characterized by a region of intense staining extending above and below the injection level, similar, but more pronounced in surface view than that in class 3B trees. The streaking effect observed in the outer wood of slightly to moderately diseased trees was absent in heavily diseased material.

Despite the presence of apparently normal foliage in the lower crowns and scattered leaves in the upper branches of class 4A material, the upward movement of the dye solution was very much restricted. In class 4A and 4B trees, adventitious branches situated 20 to 25 ft. above the forest floor are common,

and frequently the only coloration visible in longitudinal and transverse sections of the upper boles of these trees was due to "streaks" of dye in the newer growth layers, marking the paths of moisture movement to the adventitious organs. Heavily diseased trees ranged from 36 to 64 ft. in height, with diameters at breast height of 5 to 12 in. Despite uptake periods ranging from 23 to 97 hr., the absorption of the dye solution was very much reduced.

The observed trends of moisture movement in apparently healthy trees suggested that the explanation for the unusual patterns of staining noted in diseased birch was quite reasonably to be sought on the structural level. However, microscopic examination of the tissues of diseased material exhibiting the anomalous patterns described above, when compared with homologous sections of healthy material, failed to reveal any histological basis for the patterns which were observed. The adequacy of a technique such as this for the localization and identification of factors tending to obstruct the movement of moisture in woody stems is, however, open to question. Therefore, further evidence of structural influences was sought by subjecting sections of the boles of healthy and diseased stems to a simplified type of flow test.

Freshly cut, 4-ft. sections of the boles of healthy and diseased material, both injected and untreated, were inverted and suspended vertically on a wooden frame. Frustrums were then secured to the morphologically basal ends of these sections, and dye solution, under the influence of gravity, allowed to move through the samples. Unhealthy material prior to treatment was closely examined, and the abnormal staining patterns exhibited by the sections, following injection, were clearly blocked out by means of indelible markings. Following the passage of approximately 500 ml. of the solution through each section, the sample was removed from the frame, cut into 12 in. lengths, and the resulting conduction pattern closely examined. This technique permitted the testing and subsequent examination of a number of samples from each tree, as well as from trees in various stages of vigor. Tests were made of sections of the boles of healthy material, of unhealthy material showing unusual patterns of staining, and of sections of the boles of unhealthy, injected stems above the level to which the dye solution had risen. Uniform results were obtained in all tests. The dye solution moved uniformly over the entire cross section of the sapwood of the experimental material, and no evidence of obstructions to the passage of moisture through these samples could be obtained.

2. Moisture Distribution Studies

Studies of the distribution of moisture in healthy and diseased yellow birch were initiated in 1949 and continued until the early summer of 1951. Summarized data dealing with the water economy of butts, middles, and tops of healthy and diseased trees over the growing season are presented in Table II. Statistical analyses were made of these data in an effort to assay the significance of differences in moisture content within and between crown injury

TABLE II

DISTRIBUTION OF MOISTURE IN BUTTS, MIDDLES, AND TOPS OF HEALTHY AND DISEASED BIRCH STEMS. MOISTURE CONTENT EXPRESSED AS A PERCENTAGE OF THE DRY WEIGHT OF WOOD SAMPLE

	Healthy[1]				2B				3A				3B				4			
	Outer Sapwd.	Inner Sapwd.	Diff.	Heart	Outer Sapwd.	Inner Sapwd.	Diff.	Heart	Outer Sapwd.	Inner Sapwd.	Diff.	Heart	Outer Sapwd.	Inner Sapwd.	Diff.	Heart	Outer Sapwd.	Inner Sapwd.	Diff.	Heart
June Butt	59	59	—	72	58	57	+ 1	79	53	60	− 7	75	74	76	− 2	95	84	82	+ 2	91
Middle	62	62	—	65	69	69	—	75	60	62	− 2	71	78	81	− 3	100	56	71	−15[2]	88
Top	60	62	− 2	64	72	68	+ 4	74	67	70	− 3	75	60	71	−11	89	47	59	−12[2]	79
No. of trees			3				5				2				4				6	
July Butt	56	59	− 3	80	50	53	− 3	73	57	61	− 4	84	66	67	− 1	80	79	75	+ 4	83
Middle	67	67	—	75	62	61	+ 1	73	66	70	− 4	74	63	67	− 4	75	65	72	− 7	88
Top	71	68	+ 3	72	62	61	+ 1	73	70	70	—	74	63	68	− 5	76	52	60	− 8	79
No. of trees			11				11				7				8				6	
Aug. Butt	65	65	—	73	60	62	− 2	73	63	64	− 1	74	68	67	+ 1	79	89	80	+ 9	84
Middle	73	72	+ 1	76	74	72	+ 2	73	71	73	− 2	78	66	69	− 3	75	65	72	− 7	82
Top	71	71	—	78	74	70	+ 4	71	66	69	− 3	76	48	57	− 9[2]	73	51	54	− 3	73
No. of trees			10				7				8				8				18	

[1] *Includes class 1A, 1B, and 2A trees.*
[2] *Difference significant at 10% level.*

classes during the growing season. However, owing primarily to the small size of the sample, the results of these analyses were of limited value, and proved useful only in bringing into prominence differences which had already been emphasized by more qualitative procedures.

It will be recalled that identical staining patterns characterized trees of classes 1A–2B inclusive. Reference to Table II indicates that an almost similar situation held true with reference to the distribution of moisture in trees of these crown injury categories. In class 1A–2B material, the outer sapwood commonly contained slightly more moisture than the inner, both areas being considerably drier than the heartwood. The butts of these trees proved to be drier than both the middles and tops throughout the entire growing season, a relationship apparent in both inner and outer sapwood, the upper boles being commonly, but not invariably, richer in moisture than the crowns.

Clear-cut differences in the patterns of moisture distribution were found to separate trees of classes 1A–2B from those of classes 3A and 3B. It may be observed (Table II) that in trees of the latter classes, the outer sapwood was consistently drier than the inner, both regions appearing much drier than the heartwood. In June and July the inner and outer sapwood of the crowns of class 3A trees proved wetter than homologous regions of the upper boles and butts. However, a gradual drying-out of the crowns of class 3A trees became manifest in August, with the moisture content of the tops falling below that of the upper boles. The crowns of class 3B material were consistently found to be the driest regions of these trees, a relationship again apparent in both the inner and outer sapwood. During the course of the growing season, the moisture content of the upper boles of class 3B trees dropped markedly, and in company with the tops, indicated a continued drying-out of these regions of the trunk.

With regard to the distribution of moisture in class 4A and 4B material, reference should again be made to the patterns of staining observed in trees of these injury categories. The "sump-like" activity characteristic of the lower boles of such material has already been noted. This situation is reflected in the distribution of moisture in the butts of trees of these classes, the data indicating the presence of large amounts of moisture in a static stage, a situation in very marked contrast to that characteristic of healthy and less heavily diseased material. The levels of water content and the patterns of moisture distribution in the inner and outer sapwood of the upper boles and crowns of heavily diseased trees are indicative of the virtual cessation of water conduction in these regions of the trunk.

3. Root Studies

The cumulative results of root excavation studies undertaken in 1947, 1948, and 1950 are outlined in Table III and Fig. 1. A definite relationship of a complex, curvilinear nature between percentage rootlet mortality and crown injury class is at once apparent from these data. Attention is invited to the

TABLE III

ROOTLET MORTALITY IN HEALTHY AND DISEASED YELLOW BIRCH

Injury class	No. of trees	Percentage rootlet mortality		
		Min.	Av.	Max.
1A	21	11	20	42
1B	23	—	26	41
2A	10	11	21	33
2B	21	14	27	51
3A	21	20	38	63
3B	22	23	43	75
4A	21	36	55	92
4B	7	42	70	89
5A	1	—	100	—

abnormally high rootlet mortalities characteristic of apparently healthy trees, to the range of rootlet mortality within a given injury category, and to the overlap in mortality between crown injury classes.

Statistical analyses of these data reveal that rootlet mortality in class 1A, 1B, 2A, and 2B trees is significantly lower than that in class 3A, 3B, and 4A material. While no significance may be attached to differences in rootlet mortality in class 3A and 3B material, trees of both of these injury classes have significantly lower rootlet mortalities than class 4A material.

Discussion

The results gained from the foregoing survey of the moisture economy of yellow birch have been of great value in the clarification of the true nature of the birch problem. The available, cumulative, circumstantial evidence reveals that abnormally high rootlet mortalities in apparently healthy trees may constitute the initial indication of a diseased condition in the species. Likewise, the range in rootlet mortality within a given injury category and the overlap between crown injury classes together suggest an immediate explanation for the very pronounced variation in the rates of decline and the erratic patterns of deterioration which characterize the disease on the individual tree level. The data presented in Table III and Fig. 1 indicate that the reaction of the individual tree to a given percentage rootlet mortality is extremely variable, and conversely, to achieve a particular disease level, a variety of conditions, apparently varying from tree to tree, must be fulfilled. Under certain conditions the root system of a yellow birch tree appears to be of sufficient size to allow a moderate reduction in absorbing surface area before the aerial portions of the stem are affected, individual trees showing much or little tolerance in accordance with a number of factors which are not understood at present (compare for example 41% mortality in a class 1A tree with 23% in a class 3B tree).

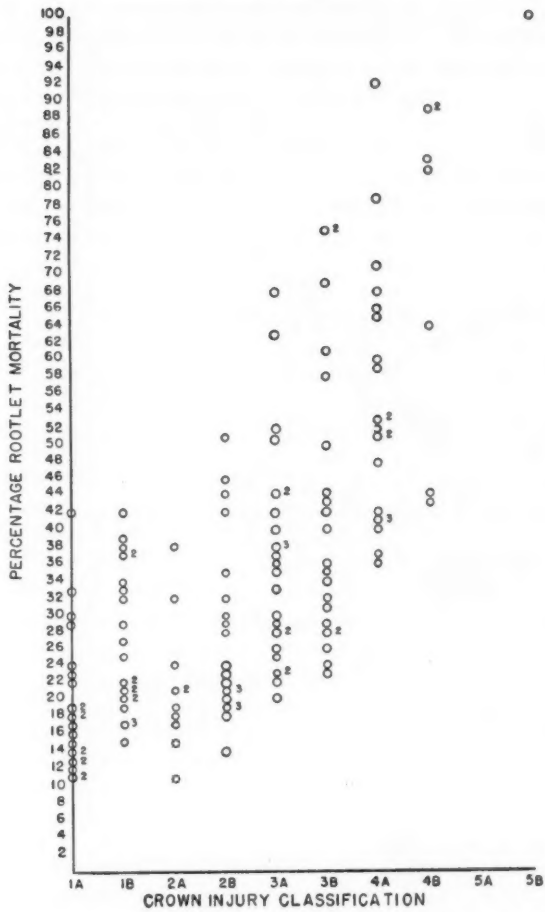

FIG. 1. The relationship of percentage rootlet mortality to crown injury class in yellow birch; duplicate observations included.

Clearly defined differences in trend have been found to separate the water relationships of the aerial portions of healthy and diseased yellow birch. These differences, brought into prominence by two semi-independent lines of investigation have proved mutually valuable in the analysis of the characteristics of decline within crown injury classes. Injection studies have led to the establishment of well-defined staining patterns within crown injury categories. Similarly, clearly marked differences in trend have been noted in the distribution of moisture in the butts, upper boles, and crowns, and in the inner and outer sapwood of healthy and diseased material, which parallel the variations

observed in the staining patterns of trees in various stages of decline. These results are clearly indicative of an implicit relationship between disease levels and the over-all moisture economy of the species. The gradual drying-out of the functional wood, and later of the upper boles and crowns, which accompanies the progressive decline of the individual tree is apparently directly attributable to inadequate supplies of moisture, suggesting that the locus of action of the disease in the first instance is in the roots. This hypothesis is strengthened by the results of extended root excavation programs.

The staining patterns and the trends in moisture distribution noted in apparently healthy material approximated for the most part the results to be anticipated from a priori considerations, the observed patterns being in complete accord with classical concepts of water conduction in large woody plants. However, the unusual patterns traced by the injection medium in moving upwards in slightly to moderately diseased trees revealed a situation which the author has not found described elsewhere in the literature. In class 3A–3B trees the failure of the dye solution to move through the newer growth layers appears to be closely linked with the relatively drier outer sapwood characteristic of this material. As noted previously, structural factors cannot be invoked to account for the aberrant staining reactions typical of slightly to moderately diseased material. The results obtained are suggestive of the presence of abnormal amounts of gas in the outer sapwood of trees of these crown injury classes, due perhaps to widespread rupture of stretched water columns under conditions of reduced absorption.

Heavily diseased material revealed deviations from the normal patterns of staining which were not entirely unexpected as a consequence of the marked decrease in the transpiring surface area of these trees. The remaining foliage of the upper branches and lower crowns of class 4A and 4B trees, exclusive of that of adventitious origin, appears to exercise no influence on water conduction, the marked curtailment in the upward movement of moisture being reflected in the levels of moisture content and the patterns of moisture distribution in the upper boles and crowns of these trees. This marked reduction in transpiration losses, coupled with an active movement of moisture into the lower boles of these trees (despite their very high rootlet mortalities) leads to the development of high moisture levels in the butts of class 4A and 4B material.

A synthesis of the results of the foregoing survey of the water relationships of healthy and diseased yellow birch reveals well-marked differences in the moisture economy of trees in various stages of decline. These differences, involving both the patterns of moisture movement and storage, are indicative of an implicit relationship between disease levels and the over-all water economy of the species. Evidence derived from several independent lines of investigation has suggested that the locus of action of the disease, in the first instance, is in the roots, and investigations are now being carried on in Nova Scotia with a view to the identification of the factor or complex of factors which has implemented the initial widespread injury to the species. The abnormally

high rootlet mortalities characteristic of apparently healthy material are strongly suggestive of the presence of a root organism of primary parasitic significance, or an environmental disturbance of major proportions. The failure to attribute a primary influence to any pathogen thus far isolated and investigated has focused attention upon the ecological aspects of the problem, and a comprehensive study of the climatic background of dieback has been initiated to explore possible correlations between major environmental fluctuations and concomitant variations in the growth and development of native hardwood and softwood species.

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SOME FOLIICOLOUS HYPHOMYCETES[1]

By S. J. Hughes[2]

Abstract

The type species and some others of the generic names *Spilocaea* (syn. *Cycloconium*, *Napicladium*, *Basiascum*), *Fusicladium* (syn. *Megacladosporium* pro maxima parte), *Passalora*, *Pollaccia*, *Hadrotrichum*, *Asperisporium*, and *Deightoniella* are illustrated and redescribed or briefly mentioned.

Introduction

In this publication I am setting out some data concerning the morphology of the type species (and some others of systematic interest) of a few foliicolous genera of hyphomycetes, most of which are well known. Some work along these lines has been published elsewhere (15); the last publication and this present one are really the outcome of a question asked some years ago—whether *Cladosporium carpophilum* was considered suitably classified in that genus, or better in *Fusicladium*. The investigation soon expanded into one concerning the type species of foliicolous hyphomycetes in general and these further results are published in the hope that they will sort out some difficulties. Most of this work was carried out at the Commonwealth Mycological Institute, Kew.

In all the species dealt with the conidiophores arise from immersed mycelium. The conidia arise as blown-out ends of conidiophores; a plurality of conidia on single conidiophores is produced either from the blown-out apices of successive proliferations *through* old conidial scars or as blown-out ends of a succession of new growing points each in turn arising laterally to the previous conidium. In the second type of development acropetal chains may be produced.

Spilocaea

The generic name *Spilocaea* is one of the few pre-Friesian names applied originally to a foliicolous hyphomycetous parasite and although perhaps as much has been written about the type species of this genus (under another name) as about any other major plant pathogen the name *Spilocaea* has long since fallen into disuse. Berkeley (2), for instance, used the name in 1836 when he wrote up the British fungi in Smith's English Flora but in Cooke's (4) Handbook of British Fungi published in 1871 the name *Spilocaea* was omitted. In 1873 Cooke (5) noted that *S. pomi* Fr. had made its appearance in the autumn of that year 'in what would seem to be stronger force than heretofore, threatening some crops with destruction.'

[1] *Manuscript received April 27, 1953.*
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[2] *Mycologist. Formerly Assistant Mycologist at the Commonwealth Mycological Institute, Kew, Surrey, England.*

Fries (8) first mentioned the name in 1819 with a description which is insufficient to validate it:

'*Spilocaea*. Fries fung. nox. Typus: *Spil. pomi*, maculas latas nigras in pomis Mali silvestris efformans.'

In 1825 Fries (9) supplied the following diagnoses:

'*Spilocaea*. Sporidia simplicia, subglobosa, sibi invicem & matrici adnata, epidermidis tenerrima pellicula secedente nuda. In Pomis vivis. (Fries Nov. Fl. Suec. V).

'Sporidiis passim seriatis Mucedinem aemulatur, eisdemque matrici tenaciter infixis Epochnium revocat. Maculas nunc latas, immo totum fructum ambientes, qui tum vix a Spermoedia distinguendus!, nunc minutas stellatas efformat.'

Also in 1825 Link (20) compiled *Spilocaea* and *S. pomi* with presumably his own description—'character ex sicco, Misit amicissimus Fries.' Link (20) described a second species *S. scirpi* Link 'in caulibus Scirporum siccis in Europa, nec non in Aegypto (v.v.).' As far as I know this species has not been adequately redescribed. In 1829 Corda (6) redescribed and figured *S. scirpi* but not to the extent that the fungus can be placed even generically.

In 1832 Fries (10) compiled *Spilocaea* with the two species *S. epiphylla* Fr. and *S. pomi* Fr. whilst *S. scirpi* Link is mentioned as a footnote. *Spilocaea epiphylla* was described on leaves of '*Pyrus*, *Malus*, etc.' from France but Prof. J. A. Nannfeldt kindly informed me that there are no collections at Uppsala, Sweden, assigned by Fries to this name. Fries (10) described *S. pomi* anew and stated that 'Nullum pomum silvestre ab hac immune vidimus; passim in hortensibus.' Fries cited the collection Scleromyceti Suec. no. 260 which I have been able to examine through the kindness of Professor Nannfeldt. I consider *S. pomi* Fr. ex Fr. to be the type species.

In 1886 Saccardo (26) included *Spilocaea* '(*S. pomi* Fr., *S. opuntiae* Rab., *S. concentrice* Schw., *S. epiphylla* Fr., *S. scripi* Link)' amongst the 'Genera dubia vel excludenda.'

It is interesting to note that Lind (18) made the combination *Fusicladium pomi* (≡ *Spilocaea pomi*) disregarding the fact that *Spilocaea* antedates *Fusicladium*.

Fries's Scleromyceti Suec. no. 260 sub *Spilocaea pomi* on apple skins is illustrated in Fig. 1 and I am unable to distinguish it from collections of

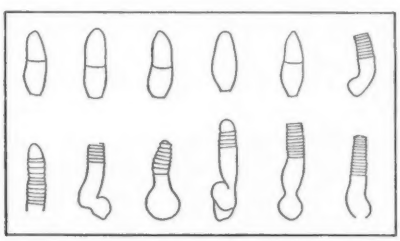

FIG. 1. *Venturia inaequalis*, conidiophores and conidia; ×500.

conidial *Venturia inaequalis*, the apple leaf- and fruit-scab fungus. The conidial state of this species can therefore be referred to as the *Spilocaea* conidiophores and conidia.

Three species with *Spilocaea* conidial fructifications.

1. **Venturia inaequalis** (Cooke) Wint. apud Thümen in Mycotheca universalis no. 261. 1875, emend. Aderh.
   ≡ *Sphaeria inaequalis* Cooke in J. Botan., Lond. 4 : 248. 1866.
   ≡ *Endostigme inaequalis* (Cooke) Syd. in Ann. Mycol. 21 : 173. 1923.
   ≡ *Spilosticta inaequalis* (Cooke) Petrak in Ann. Mycol. 38 : 193. 1940.
   = *Spilocaea pomi* Fries in Nov. Fl. Suec. . . . p. 79, 1819, and Syst. orb. veget., p. 198. 1825.
   ≡ *Spilocaea pomi* Fr. ex Fr. in Systema mycologicum, 3 : 504. 1832.
   ≡ *Fusicladium pomi* (Fr.) Lind in Danish Fungi. p. 521. 1913.
   = *Helminthosporium pyrorum* Libert (pro parte in *Pyri mali*) in Plantae crypt. Arduennae, Fasc. 2 : no. 188. 1832.
   = *Cladosporium dendriticum* Wallr. in Flora crypt. Germaniae, Part 2 : 169. 1833.
   ≡ *Fusicladium dendriticum* (Wallr.) Fuckel in Symbolae Mycologicae, 357. 1870.
   = *Napicladium sorauerí* Thümen in Mycotheca universalis, no. 91. 1875.
   ≡ *Fusicladium dendriticum* var. *sorauerí* (Thüm.) Sacc. in Sylloge fungorum, 4 : 346. 1886.

This common species is also illustrated in Fig. 2, drawn from I.M.I. 17633(*a*) on apple leaves, East Malling, Kent, England, 4.ix.1947 (P.C.R. Webb). Subcuticular mycelium is present and the conidiophores are markedly annellate owing to the conidia being produced as the blown-out apices of successive proliferations through the conidial scars.

Note on Napicladium: In January 1875 Thümen (28) published his new generic name *Napicladium* for the single [type] species *N. sorauerí*. Also in 1875 he issued Mycotheca universalis no. 91 sub *N. sorauerí* with generic and

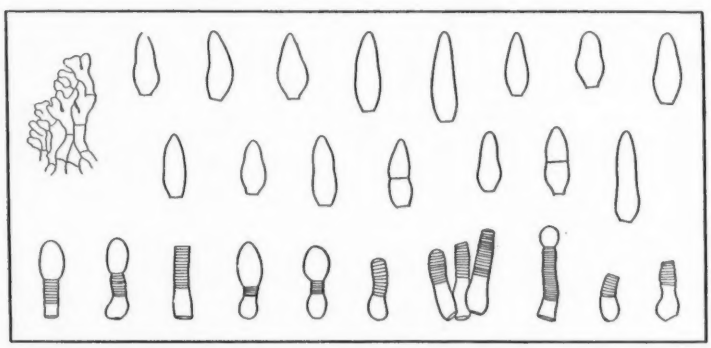

FIG. 2. *Venturia inaequalis*, subcuticular mycelium, conidiophores, and conidia; ×500.

species diagnoses which differ little from those published in Hedwigia. The exsiccatum very probably represents the type collection; if not, it is at least authenticated for this name. Thümen (28) explained that the new generic name was published because his fungus had mostly 1-septate conidia whereas in the type species of *Fusicladium* Bon., *F. virescens* Bon., the conidia were claimed to be continuous. The Herb. R.B.G. Kew copy of Thümen's exsiccatum has been examined and I cannot distinguish the fungus on the skin of the apple fruit from the *Spilocaea* conidial apparatus of *Venturia inaequalis*.

Saccardo (26) included the type species of *Napicladium* as *Fusicladium dendriticum* var. *soraueri* (Thüm.) Sacc. but nevertheless made use of the generic name *Napicladium* without its type species. I regard *Napicladium* as a synonym of *Spilocaea*. One of the species commonly referred to as *N. arundinaceum* was reclassified by Hughes (15) in 1952 (see p. 574).

2. **Spilocaea eriobotryae** (Cav.) comb. nov.
   ≡ *Basiascum eriobotryae* Cav. in Atti Ist. Botan. Pavia, II, 1 : 433. 1888.
   ≡ *Fusicladium eriobotryae* (Cav.) Cav. apud Briosi & Cavara in I funghi parassiti d. piante coltivate od utili, no. 186. 1892.
   ≡ *Fusicladium melanconioides* Ferraris [nom. nov.] in Ann. Mycol. 7 : 284. 1909.

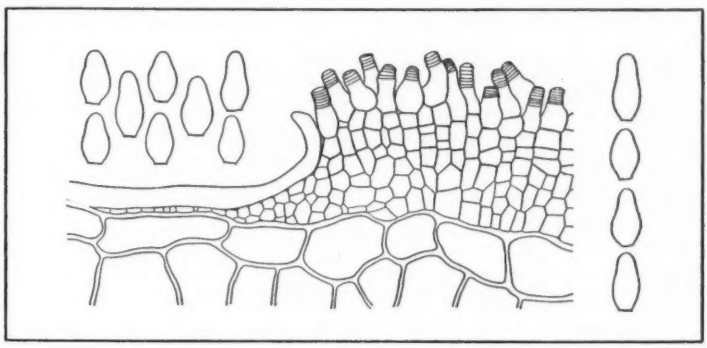

FIG. 3. *Spilocaea eriobotryae*, subcuticular mycelium, conidiophores, and conidia; ×500.

The Briosi & Cavara exsiccatum no. 186 (I.M.I. 7582) is authenticated for this species name and is illustrated in Fig. 3. Subcuticular mycelium is present and this becomes locally thickened to form a pustule on which the characteristic *Spilocaea* conidiophores are produced. v. Höhnel (14) in 1923 considered this to be a form of *Fusicladium dendriticum* but he did not reduce Cavara's species to varietal rank.

Note on Basiascum: The generic name *Basiascum* was published by Cavara (vide supra) for the single type species *B. eriobotryae* and this author subsequently transferred it to *Fusicladium*. It appears to me that the fungus is best referred to *Spilocaea* Fr. of which *Basiascum* is a synonym.

3. **Spilocaea oleaginea** (Cast.) comb. nov.

≡ *Cycloconium oleagineum* Cast. in Catalogue des plantes . . . . environ de Marseilles, p. 220, 1845 [as *oleaginum*].

Fig. 4 and the description that follows are based on a collection by R. M. Nattrass, on living leaves of the olive, Nicosia, Cyprus, 20.iii.1931 (I.M.I. 7445).

Visible colonies formed on the upper surface of leaves, are gray to black depending on the density of the conidiophores and conidia, about 5 mm. in diameter or effuse and covering the whole leaf surface.

The *mycelium* is composed of hyaline, septate, frequently branched, radiating hyphae, 2.5-8 μ wide* which may be closely compacted and when viewed from above seems to form a continuous immersed radiating plate. According to Miller (22), who used special techniques, the mycelium was found in an outer epidermal layer of small cells and not under the cuticle. In fallen leaves he found the fungus to grow extensively in the host tissues.

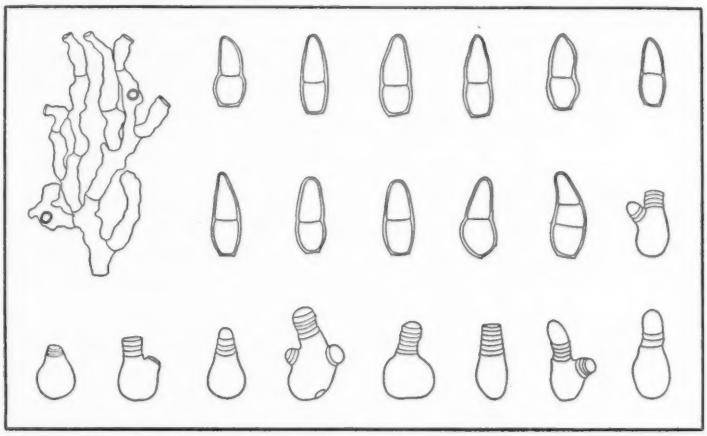

FIG. 4. *Spilocaea oleaginea*, mycelium, conidiophores, and conidia; ×500.

The *conidiophores* arise by the blowing-out from the immersed hyphae of a bulb through the 'cuticle'; they are crowded or widely separated, at first subglobose and about 8-10 μ in diameter, later flask-shaped with a swollen base 8-15 μ wide with the cylindrical neck irregularly and closely annellated. They are continuous, thick-walled, usually straight and erect, up to 28 μ long, pale brown to dark brown below but paler above, sometimes smooth but usually coarsely roughened, and sometimes two or three necks have developed on one conidiophore, each neck with its characteristic annellations.

The *conidia* arise singly as the blown-out ends of conidiophores and of their successive proliferations through the conidial scars. They are shortly

* *All measurements given in this paper were made from preparations in lactic acid, with or without cotton blue.*

obclavate, rounded at the apex, somewhat flattened at the basal scar which is surrounded by a ridge, 1-septate, slightly constricted, thick-walled, verrucose, sometimes irregularly striate, yellow-brown to pale brown, 19-28 × 9-12 (mostly 21-26 × 10-12) μ, sometimes 2-septate and 26-30 × 9.5-11 μ.

Note on Cycloconium: This generic name was published by Castagne (vide, supra) for the single [type] species *C. oleagineum* which he described on living leaves of *Olea europea* collected at Marseilles, France. At present the fungus is widely distributed—the Mediterranean region, East and South Africa, Australia, South America, and California. The statement by Miller (22) that the mycelium is subcuticular cannot I believe exclude this fungus from *Spilocaea* Fr. of which I regard *Cycloconium* as a synonym.

In view of the foregoing I propose the following synonymy.

Spilocaea Fr. ex Fr.
= *Cycloconium* Castagne
= *Napicladium* Thümen
= *Basiascum* Cavara.

Fusicladium

In 1851 Bonorden (3) published his generic name *Fusicladium* for his single [type] species *F. virescens* with the following diagnoses and with an illustration which is reproduced here as Fig. 5: '*Fusicladium* Bon. simple, septate hyphae carry at their pointed apices, of which there may sometimes be two, one or two spindle-shaped, simple spores. 1. *Fusicladium virescens* forms light brown mats consisting of short, non-septate threads which arise from the mycelium in the living leaf cells. The spores are transparent and greenish. Occurs in gardens on cultivated [veredelten] apple trees. The parenchyma of the leaves where the fungus grows is dark and penetrated by mycelium. The young spores are at first round, then oval, and only spindle-shaped at maturity' (translation).

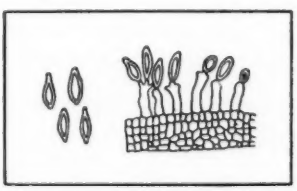

FIG. 5. *Venturia pirina*, conidiophores and conidia after Bonorden (3) sub *Fusicladium virescens*; slightly reduced from original.

As far as I am aware Bonorden's type collection, if it is still in existence, has not been re-examined; however, it is generally accepted that his illustration and diagnosis refer to one of the scab-fungi, one of the *Fusicladium* species as the name has been currently used in plant pathological literature. Bonorden's fungus was described on apple leaves so one would except the fungus to be conidial *Venturia inaequalis* (Fig. 2).

In 1923 Höhnel (14) identified *Fusicladium virescens* with *F. dendriticum* (= *Venturia inaequalis* = *Spilocaea pomi*) but Bonorden's description and illustration (Fig. 5) lend no support to this. Bonorden figured and in effect described the conidiophores as denticulate at the apex and one particular conidiophore he figured with three denticles, two of which carry single conidia; but in '*F. dendriticum*' the conidiophores are of the *Spilocaea* type with close annellations (Fig. 2), the apex of the conidiophores being flat and incapable of supporting two conidia at one time by virtue of the mode of conidium development. I am inclined to the view, therefore, that Bonorden misidentified the leaves of his original collection, indeed not a difficult thing to do; the leaves may well have been those of the pear because the pear-scab fungus (= *Venturia pirina* = '*Fusicladium pirinum*') produces denticulate conidiophores (Fig. 6). Both Saccardo (26) and Lindau (19) cited *F. virescens* as a synonym of '*F. pirinum*' as did Viennot-Bourgin (29). The generic name *Fusicladium* has been used without any distinction by most authors for fungi which produce the *Venturia inaequalis* or annellate type and the *Venturia pirina* or denticulate type of conidiophores. Notwithstanding the apparent generic identity of the ascigerous states it seems best, to me at least, for the annellate conidiophores to be referred to the form genus *Spilocaea* and the denticulate conidiophores to the form genus *Fusicladium*. Should the differences in the methods of successive conidium production not be regarded as a generic distinction then it will be necessary on grounds of priority to use the name *Spilocaea* Fr. instead of *Fusicladium* Bon. The name *Fusicladium* cannot be applied to both types of conidiophores!

Although Viennot-Bourgin (29) accepted the identity of *F. virescens* Bon. with conidial *Venturia pirina* he nevertheless used the name *Fusicladium* for the annellate [or *Spilocaea*] type of conidiophores; at the same time he proposed the name *Megacladosporium* for five species including '*M. pirinum*' (='*Fusicladium pirinum*'). Although his use of the generic name *Fusicladium* was wrong I would like to draw attention to the fact that he regarded the two types of conidium structure and development as deserving different generic names. *Megacladosporium* is further discussed on p. 569.

Four species with *Fusicladium* conidial fructifications.

1. **Venturia pirina** Aderh. in 'Landwirthsch. Jahrb. 25 : 875. 1896.'
   ≡ *Endostigme pirina* (Aderh.) Syd. in Ann. Mycol. 21 : 173. 1923.
   = *Helminthosporium pyrorum* Libert (pro parte in *Pyri communi*) in *Plantae crypt. Arduennae*, Fasc. 2; no. 188. 1832.
   ≡ *Fusicladium pyrorum* (Lib.) Fuckel in Symb. mycologicae, p. 357, 1870 (ex errore sub '*Fusicladium pyrinum*').
   ≡ *Megacladosporium pyrorum* (Lib.) Viennot-Bourgin, in Les champignons parasites des plantes cultivées, Vol. I : 489. 1949 (ex errore sub '*Megacladosporium pirinum*').
   = *Fusicladium virescens* Bon. in Handbuch der allgemeinen Mykologie, p. 80, 1851.

This fungus is too well known to need another description so I include only an illustration of Krypt. exsicc. a Mus. Palat. Vindobon. no. 1496 on leaves of *Pyrus communis* sub '*Fusicladium pirinum*'. Fig. 6 shows some subcuticular mycelium, denticulate conidiophores, and conidia.

Although Libert described her fungus with the epithet '*pyrorum*', Fuckel (vide supra) erroneously used '*pyrinum*' when he made the new combination; '*pyrinum*' or '*pirinum*' have been used ever since—erroneously.

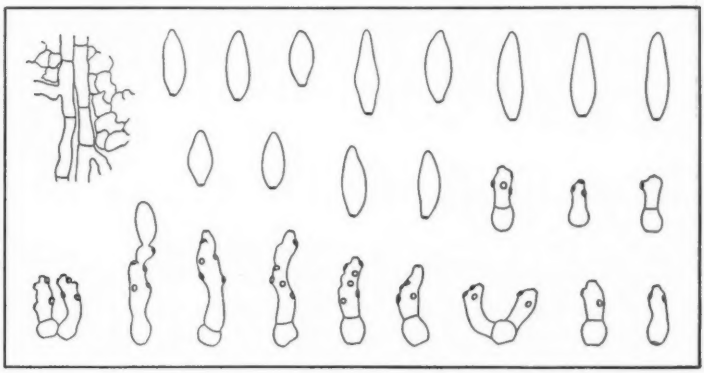

FIG. 6. *Venturia pirina*, subcuticular mycelium, conidiophores, and conidia; ×500.

2. **Venturia cerasi** Aderh. in Landwirthsch. Jahrb. 29 : 541. 1900.

= *Acrosporium cerasi* Rabenh. in 'Braun, Ueber einige neue oder weniger bekannte Krankheiten der Pflanzen, p. 16, Berlin. 1854.'

≡ *Fusicladium cerasi* (Rabenh.) Sacc. in Sylloge fungorum, 4 : 346. 1886.

≡ *Cladosporium cerasi* (Rabenh.) Aderh. in Zentr. Bakt. 2 Abt., 7 : 656. 1901.

≡ *Megacladosporium cerasi* (Rabenh.) Viennot-Bourgin in Les champignons parasites des plantes cultivées, Vol. I : 537. 1949.

Fig. 7 was drawn from a collection by R. M. Nattrass, on living leaves of *Prunus* sp., Nicosia, Cyprus, 4.iv.1931 (I.M.I. 7559); it shows some subcuticular mycelium, denticulate conidiophores, and conidia. Viennot-Bourgin (29) figured this species with conidia possessing scars at both ends; this was not observed in the collection from Cyprus.

3. **Venturia crataegi** Aderh. in Ber. d. deutsch. botan. Gesellsch. 20 : 200. 1902.

≡ *Endostigme crataegi* (Aderh.) Syd. in Ann. Mycol. 21 : 173. 1923.

= *Fusicladium crataegi* Aderh. in loc. cit. supra.

≡ *Megacladosporium crataegi* (Aderh.) Viennot-Bourgin in Les champignons parasites des plantes cultivées, Vol. I : 539. 1949.

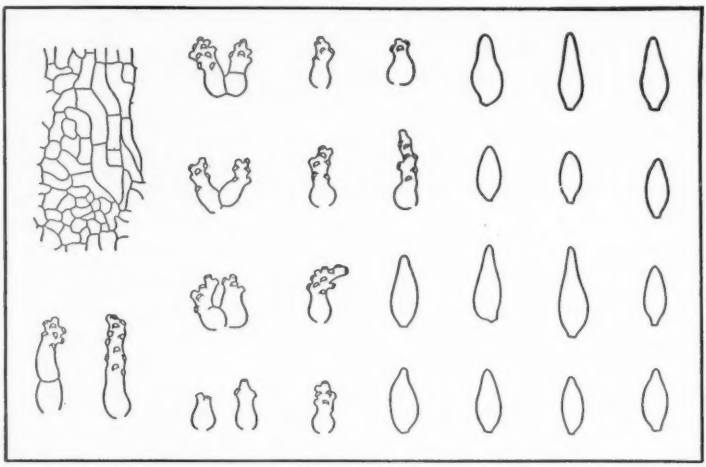

FIG. 7. *Venturia cerasi*, subcuticular mycelium, conidiophores, and conidia; ×500.

Fig. 8 was drawn from Sydow, Mycotheca germanica no. 45 sub *Fusicladium crataegi* on *Crataegus oxyacantha*, Germany, 15.iii.1902, and it shows very slightly denticulate conidiophores and 1-septate conidia. The conidiophores arise from subcuticular mycelium as in the two preceding species.

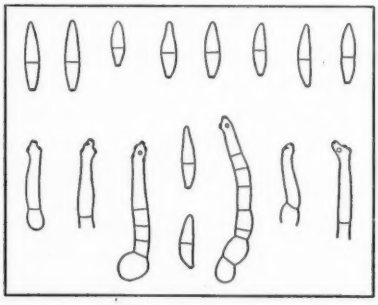

FIG. 8. *Venturia crataegi*, conidiophores and conidia; ×500.

4. **Fusicladium carpophilum** (Thüm.) Oudem. in Versl. K. Akad. Wet. Amsterdam, 388. 1900.

≡ *Cladosporium carpophilum* Thüm. in Oesterr. Botan. Zeitschr. 27 : 12. 1877.

≡ *Megacladosporium carpophilum* (Thüm.) Viennot-Bourgin in Les champignons parasites des plantes cultivées, Vol. I : 489. 1949.

Fig. 9 was drawn from the Herb. R.B.G. Kew copy of Ellis and Everhart, North American Fungi (Ser. 2), no. 3588, sub *Cladosporium carpophilum*, on peach fruits, Ontario. Subcuticular mycelium is present and conidiophores

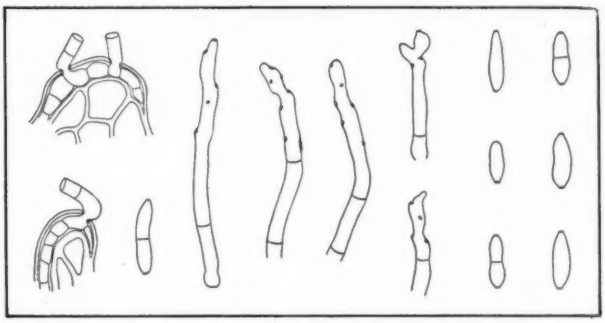

FIG. 9. *Fusicladium carpophilum*, subcuticular mycelium, conidiophores, and conidia; ×500.

arise from it; much subepidermal mycelium is also produced later. The very slightly denticulate conidiophores are similar to those of the type species of *Fusicladium* in that they produce conidia singly as the blown-out ends of successively produced growing points thereby being quite different from *Cladosporium* in which the conidiophore is of determinate length. The conidia are more or less regular in size and develop simple acropetal chains. I see no characters for excluding this species from *Fusicladium*. The subcuticular development of the peach fungus with the production of conidiophores on twigs, fruits, and leaves has been described by Keitt (17).

Two species excluded from *Fusicladium*.

1. *Fusicladium destruens* Peck (25). This is a *Heterosporium* and I am unable to distinguish an authenticated collection, preserved in Herb. N.Y. State Museum, Albany, N.Y., from DAOM 35168 on *Scirpus* stems, Sydney, Vancouver Island, 1916, J. Macoun, which was determined by J. Émile Jacques in 1942 as *Heterosporium maculatum* Klotzsch.
2. *Fusicladium robiniae* Shear is classified in *Passalora* on p. 572.

Note on Megacladosporium: Viennot-Bourgin published this generic name in 1949 for five species without designating the type. These are:

M. carpophilum (≡ *Fusicladium carpophilum*, Fig. 9),
'*M. pirinum*' (≡ *F. pyrorum*, Fig. 6),
M. cerasi (≡ *F. cerasi*, Fig. 7),
M. crataegi (≡ *F. crataegi*, Fig. 8), and
M. depressum (≡ *F. depressum*, Fig. 11).

Now '*M. pirinum*', *M. carpophilum*, *M. cerasi*, and *M. crataegi* are here considered to be congeneric and can be classified as *Fusicladium*, of which '*F. pirinum*' (*M. pirinum* = *Fusicladium virescens*) is the type species. Furthermore *M. depressum* is congeneric with *Passalora bacilligera* (Fig. 10) and best classified as *P. depressa* (Berk. & Br.) Sacc. The generic name *Megacladosporium*, therefore, is relegated to synonymy pro maxima parte with *Fusicladium* and pro minima parte with *Passalora*.

Passalora

The generic name *Passalora* was published by Fries (11) in 1849 but no species was mentioned although reference was made to Montagne's (23) publication. In 1856 the combination *Passalora bacilligera* [(Mont. & Fr.)] Mont. & Fr. apud Montagne (24) as '*Passalora bacilligera* M. et Fr.' was published for the first time, based on *Cladosporium bacilligerum* Mont. & Fr. apud Mont. (1836 (23)). I consider *Passalora* Mont. & Fr. to be typified by *P. bacilligera* and the genus to date from 1856.

Three species with *Passalora* conidial fructifications.

1. **Passalora bacilligera** (Mont. & Fr.) Mont. & Fr. apud Mont. in Sylloge generum specierumque cryptogarum. Paris. 1856.
   ≡ *Cladosporium bacilligerum* Mont. & Fr. apud Mont. in Ann. Sci. Nat. II, 6 : 31. 1836.

Fig. 10 was drawn from Krypt. exsicc. a Mus. Palat. Vindobon. no. 1938, on leaves of *Alnus glutinosa*, sub *Passalora bacilligera* (I.M.I. 12023).

The mycelium is found throughout the leaf thickness and not restricted to any one layer.

The *conidiophores* arise subepidermally from small stromata and emerge through the stomata in small tufts; they are simple, sometimes branched, septate, and pale brown to brown.

The *conidia* arise singly as blown-out ends of successive new growing points which develop below the previous terminal conidium; at maturity they are 1-septate, more or less obclavate, constricted at the septum, and subhyaline to pale brown.

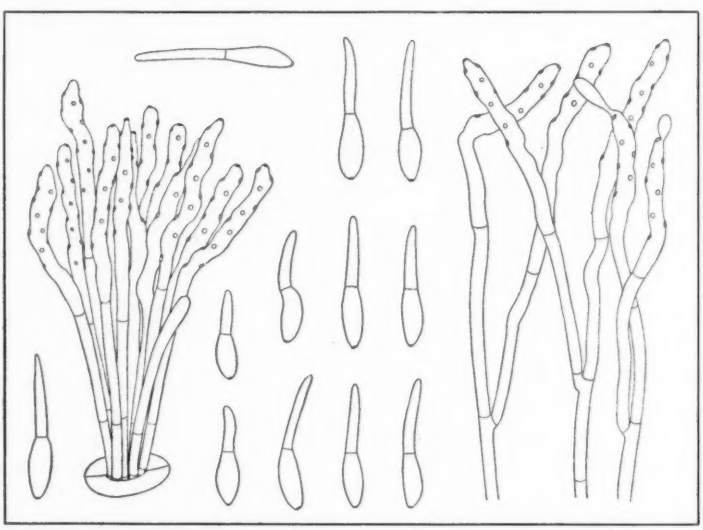

FIG. 10. *Passalora bacilligera*, conidiophores and conidia; ×500.

In 1944 Chupp and Green (Green (13)) described their new species *Cercospora alni* on *Alnus crispa* from Wisconsin, U.S., and with its rarely branched conidiophores, very pale to pale olivaceous 1-septate conidia with the lower cell inflated, there is no doubt that their new *Cercospora* is based on *Passalora bacilligera*. This is interesting because it helps one to disbelieve the supposed distinction between *Cercospora* and *Passalora*. However, *Passalora* is used in this paper for *Cercospora*-like fungi with predominantly 1-septate conidia with the lower cell somewhat swollen.

2. **Passalora depressa** (Berk. & Br.) Sacc. in Nuovo G. Bot. ital. 8 : 187. 1876.
   ≡ *Cladosporium depressum* Berk. & Br. in Ann. Mag. Nat. Hist. II, 7 : 99. 1851.
   ≡ *Fusicladium depressum* (Berk. & Br.) Roum. in Fungi Gallici exsiccati, no. 76 : 1879.
   ≡ *Megacladosporium depressum* (Berk. & Br.) Viennot-Bourgin in Les champignons parasites des plantes cultivées. Vol. II : 1488. 1949.

This fungus has been redescribed recently by Ellis *et al.* (7). Fig. 11 was drawn from I.M.I. 32193 (on *Angelica sylvestris*, Co. Down, N. Ireland, 16.ix.1948, G.M. Waterhouse) and shows conidiophores arising from a small subepidermal stroma. The conidiophores which bear scattered conidial scars show a tendency to unilateral thickening and curvature as in *Fusicladiella melaena* (Fuckel) Hughes and *Camptomeris albizziae* (Petch) Mason (Hughes (16)). *Passalora depressa* is one of the five species that Viennot-Bourgin (29) included in his new genus *Megacladosporium* and which can be classified in *Passalora*.

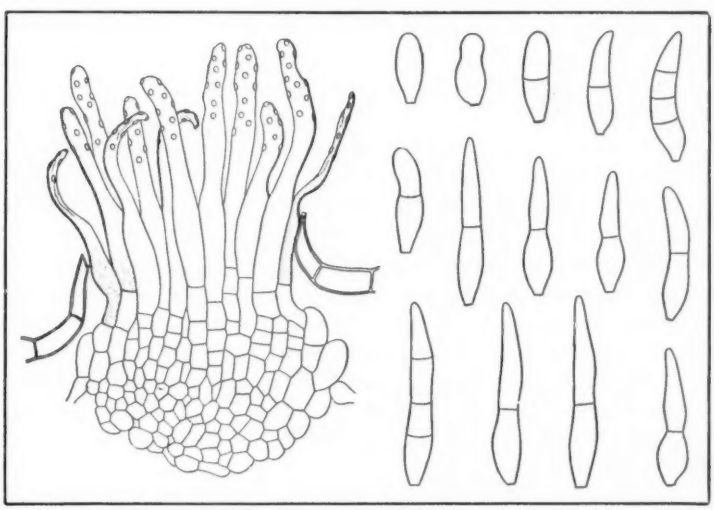

FIG. 11. *Passalora depressa*, conidiophores and conidia; ×500.

3. **Passalora robiniae** (Shear) comb. nov.

≡ *Fusicladium robiniae* Shear in Bull. Torrey Botan. Club, 29 : 452. 1902.

≡ *Camptomeris robiniae* (Shear) Ciferri in Mycopath. 6 : 25. 1951.

I have not seen the type collection but DAOM 24804 (Fig. 12) on *Robinia pseudoacacia*, Arlington Farm, Va., U.S., 7.ix.1938, collected and determined by T. J. Grant, matches the original description exactly. The conidiophores arise in tufts from substomatal stromata and bear a succession of 1-(rarely 2-) septate conidia, the lower cell being wider than the upper one. This is exactly *Passalora*.

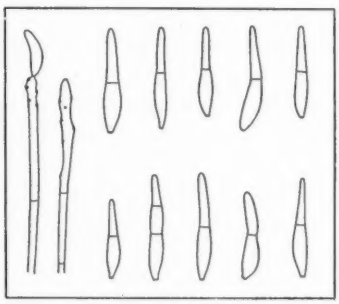

FIG. 12. *Passalora robiniae*, conidiophores and conidia; ×500.

Pollaccia

The generic name *Pollaccia* was described in 1937 by Baldacci and Ciferri (Baldacci (1)) for the single [type] species *P. radiosa* (Lib.) Bald. & Cif. (≡ *Oidium radiosum* Lib.), the well known *Populus* leaf-spotting fungus.

In 1939 Servazzi (27) differentiated two species of *Pollaccia* on *Populus*, *Pollaccia radiosa*, which he claimed to be conidial *Venturia tremulae* Aderh. and *Pollaccia elegans* Serv., which he claimed to be conidial *Venturia populina* (Vuill.) Fabric. The conidia of the former averaged 18-26 × 5-8 μ and those of the latter 35-38.5 × 11 μ.

Up to June 1952 all the collections in Herb. I.M.I. were identified as *P. radiosa* on the basis of conidium measurements. In *P. radiosa* a stroma arises within the epidermal cells of the infected leaves and sporogenous cells are formed on it (Fig. 13). The sporogenous cells have inconspicuous annellations towards the apex indicating successive proliferations through the scars left by previous conidia. The conidia are mostly 2-septate and symmetrical with a flattened basal scar with marginal frill. In 1-septate conidia, which are of the same shape as the 2-septate ones, the single septum is laid down at the distal end. Fig. 13 was drawn from I.M.I. 7599, on *Populus tremula*, Germany, 22.v.1923, A. Ludwig.

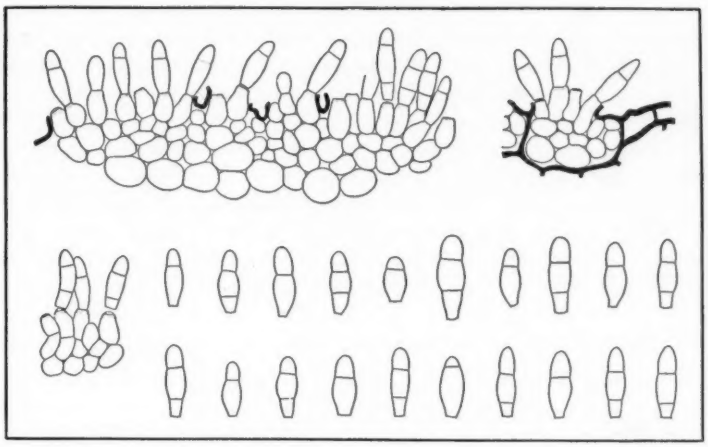

FIG. 13. *Pollaccia radiosa*, intraepidermal stroma, conidiophores, and conidia; ×500.

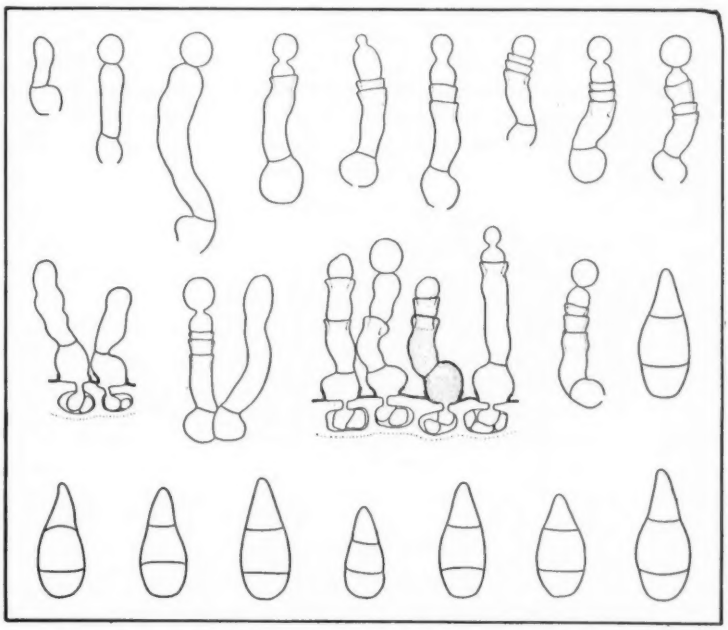

FIG. 14. *Deightoniella arundinacea*, conidiophores and conidia; ×500.

Deightoniella

This name was published by Hughes (15) for two species, *D. africana* Hughes, the type species, and *D. arundinacea* (Corda) Hughes. The second species was redescribed and figured by Ellis *et al.* (7) in 1951 (as *Napicladium arundinaceum*); these authors found the fungus to be systemic and abundant mycelium was found in sections cut at different levels throughout the roots, rhizomes, culms, and leaves. *D. arundinacea* is illustrated here in Fig. 14. The conidiophores arise from intraepidermal cells and successive conidia develop on successive proliferations through previous conidial scars. Fig. 14 was drawn from I.M.I. 5487 on *Phragmites communis*, Hickling Broad, Norfolk, England, 9.vii.1945, E. A. Ellis.

Key to Some Foliicolous Parasites with Annellated Conidiophores

The production of annellated conidiophores as a result of conidium production is common to a number of foliicolous parasites such as *Spilocaea*, *Mastigosporium*, *Stigmina*, *Pollaccia*, and *Deightoniella*. These may be distinguished conveniently as follows:

1. Conidiophores aggregated into distinct groups
   - A. Fructifications composed of groups of hyaline conidiophores each arising independently from hyphae which penetrate the outer epidermal wall and cuticle; conidia hyaline, produced in slime..... *Mastigosporium*
   - B. Fructifications composed of subepidermal or subcuticular stromata bearing dematiaceous conidiophores on exposed surface; conidia dematiaceous, dry..... *Stigmina*

2. Conidiophores effuse
   - A. Mycelium throughout leaf thickness and aggregated in epidermis but not differentiated into radiating hyphal plates..... *Deightoniella*
   - B. Mycelium almost restricted to subcuticular or intraepidermal region and differentiated into radiating hyphal plates
     - (1) Conidia more or less oval and symmetrical, usually 2-septate, or 1-septate with septum at distal end; conidiophores on intraepidermal, erumpent stromata..... *Pollaccia*
     - (2) Conidia more or less obclavate, continuous or 1-septate; conidiophores on erumpent subcuticular stromata or borne directly on subcuticular or intraepidermal hyphae on unbroken surface of epidermis..... *Spilocaea*

Hadrotrichum

This generic name was published in 1865 by Fuckel (12) for the single [type] species *H. phragmitis* Fuckel. In this species the stroma (Fig. 15) is subepidermal and bursts through the epidermis. The more or less spherical, continuous, roughened conidia arise singly as the blown-out ends of a succession

of new growing points. I have seen no illustration of this fungus which shows the conspicuous scars indicating the succession of conidia. Fig. 15 was drawn from I.M.I. 7150 on *Phragmites communis*, Cyprus, x.1933, R. M. Nattrass.

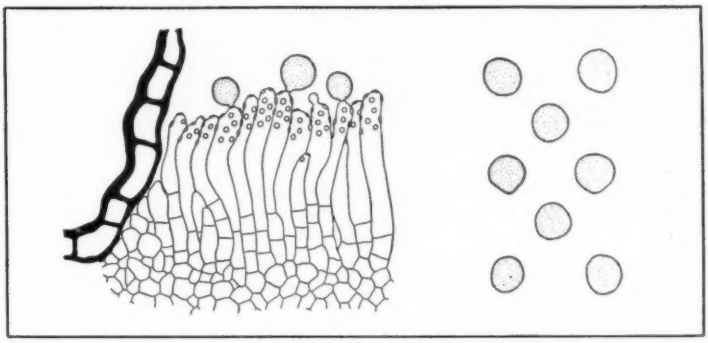

FIG. 15. *Hadrotrichum phragmitis*, conidiophores on subepidermal stroma, and conidia; ×500.

Asperisporium

The generic name was published by Maublanc (21) and *A. caricae* (Speg.) Maubl. (≡ *Cercospora caricae* Speg.) may be considered the type species; Maublanc described the ascigerous state as *Sphaerella caricae* Maubl., but no pure cultures were made to determine this.

I.M.I. 34807, on the type host, *Carica papaya* (Jamaica, iii.1949, E. B. Martyn) is illustrated in Fig. 16. The stroma is subepidermal and bursts through the epidermis; it bears crowded, short conidiophores which produce single conidia as the blown-out ends of a succession of new growing points. At maturity the conidia are 1-septate and roughened. A comparison of the type species of *Hadrotrichum* and *Asperisporium* indicates that the only character differentiating them is the septate conidia of the last named.

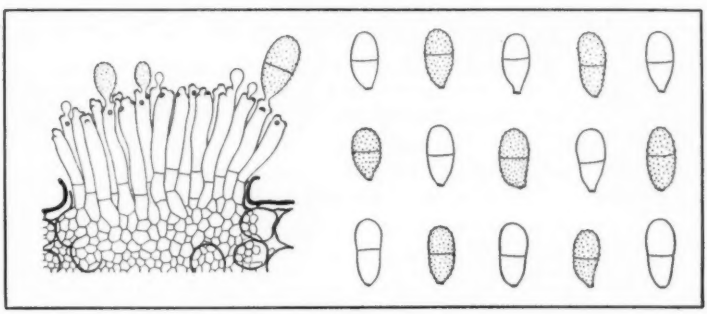

FIG. 16. *Asperisporium caricae*, conidiophores on subepidermal stroma, and conidia; ×500.

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CONIDIOPHORES, CONIDIA, AND CLASSIFICATION[1]

By S. J. Hughes[2]

Abstract

Characters of conidiophore and conidium development are used for the separation of some common temperate and a few tropical Hyphomycetes into eight Sections. The need for further studies on the precise method of conidium development is stressed because this promises to provide the most stable character for the classification of Fungi Imperfecti as a whole. Conidiophores and conidia of a large number of Hyphomycetes are figured to illustrate the various characters common to each Section.

Introduction

This paper comprises an experiment in classifying some Hyphomycetes into sections based primarily upon the different types of conidiophore and conidium development. The mononematous, synnematous, or tuberculariaceous nature of conidiophores, the form of mature conidia, their dematiaceous or mucedinous nature, their septation, and the presence or absence of slime around them are treated as subsidiary characters.

Saccardo (99) divided the Hyphomycetes into four groups: Mucedineae, Dematieae, Stilbeae (Hyalostilbeae and Phaeostilbeae), and Tuberculariеae (Tuberc. mucedineae and Tuberc. dematieae). Sections were then delimited on conidium morphology: Amerosporae, Didymosporae, Phragmosporae, Dictyosporae, Staurosporae (Asterosporae), and Helicosporae. Saccardo (100) made slight modifications of this scheme in 1906.

Most workers on Hyphomycetes are losing confidence in the major division of this group on the basis of Mucedineae/Dematieae, especially when only the conidia and the visible parts of conidiophores are taken into account. It is of interest to note that Saccardo (99) regarded *Verticicladium* Preuss as dematiaceous *Verticillium* Nees. In 1910 A. L. Smith (106) observed dark color in *V. albo-atrum* Reinke & Berth. and she seemed justified, according to the Saccardoan system, in classifying the fungus as *Verticicladium albo-atrum* (Reinke & Berth.) A. L. Smith. This combination has not been taken up and it would be agreed that too great a stress was being laid on color if *Verticillium albo-atrum* were to be separated generically from the only critically distinct *V. dahliae* Kleb., which, however, also develops color in the form of dark sclerotia (Isaac (71)). In any case *Verticillium* and *Verticicladium* have quite distinct types of conidium development (Hughes (51)).

To separate *Ramularia* Unger and *Cercospora* Fres. into the families Mucedineae and Dematieae seems to me to be wrong especially when so many *Ramularia* spp. develop conidiophores from immersed dark colored sclerotia or stromata. Numerous examples occur of the failure of such a division to separate morphologically unrelated fungi and hold together those that have

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a similar morphology. With regard to color, however, it is worth while remembering that large numbers of Hyphomycetes have brightly colored fructifications and mycelium, characters which we have learned to associate with the Hypocreales and some Basidiomycetes; examples are *Apiocrea chrysosperma* (Tul.) Syd. (= *Sepedonium chrysospermum* Fr.) and *Nectria inventa* Pethybr. (= *Acrostalagmus cinnabarinus* Corda). With further knowledge of the perfect states of Hyphomycetes color may prove to be a useful character. A further instance of confusion arising from reliance on color is given below when *Helicomyces scandens* is briefly discussed.

In the division of the Hyphomycetes into four families by Saccardo, stress was laid upon the way conidiophores are grouped or not grouped; briefly, in the Mucedineae and Dematieae they are solitary or at least separate along their length, in the Stilbeae long conidiophores are fused into synnemata, whilst in the Tuberculariеae generally short conidiophores are aggregated on stromata usually in the form of tubercles (sporodochia). The conidiophores and conidia in any one of these groups are by no means homologous. The generic name *Phragmocephala* was published by Mason and Hughes (85) in the belief that the species* whose conidiophores are solitary, in tufts on a small stroma or in synnemata, are all congeneric; in Saccardo's scheme they would be separated amongst the Dematieae, Tuberculariеae, and Stilbeae, presumably under three different generic names.

The genera *Scopulariopsis*, *Phaeoscopulariopsis*, and *Stysanus* would, under the old scheme, be classified in the Mucedineae, Dematieae, and Stilbeae respectively but the sporogenous cells and conidium development are alike and the three names, if there be need for three, should occupy neighboring positions in any classification.

In *Exosporium tiliae*, *Helminthosporium velutinum*, and *Helminthosporium stilbaceum* (Hughes (59)) the method of development of the helminthosporioid conidia is identical. The first named, however, is found amongst the Tuberculariеae, and the second amongst the Dematieae although this species and a number of congeneric ones sometimes develop groups of conidiophores on small stromata; the third species would presumably be classified in the Stilbeae although here the conidiophores are only closely pressed together and not fused along their length.

v. Höhnel (42) published his genus *Helicostilbe* for the single species *H. helicina* v. Höhnel. According to Linder (77) this is *Helicomyces scandens* Morgan; Linder showed that in an early stage of development conidiophores are solitary on repent hyphae but at maturity synnemata are formed with erect, bristle-like, brown setae. Saccardo (100) classified von Höhnel's genus in the Phaeostilbaceae although Clements and Shear (20) compiled it amongst the Hyalostilbeae.

The absence of septation or the variation in the septation of conidia, with the morphology of mature conidia, has been given too great an importance in classification. It is well known that in some genera, e.g. *Brachysporium* and

* *The term 'species' is used loosely in this paper.*

Curvularia, septation in the various species is more or less constant; in the graminicolous species assigned erroneously to *Helminthosporium* on the other hand, or in *Sporidesmium* (sensu stricto) the conidia in the different species may show great variation. On the whole it seems that the longer the conidia the more variable is the number of septa. In some genera, in the past, little importance seems to have been paid to variation in the numbers of septa; thus, in *Ramularia*, Saccardo compiled over 400 species whose conidia varied from continuous, up to 1-septate, 2-, 3-, 4-, 5-, 6-, 7-, even up to 8-septate (Hughes (43)). All the species of *Ramularia* which have been studied over a period of time usually show a considerable degree of variation in septation of the conidia composing the chains and this has been shown to be correlated with humidity.

In many fungi whose conidia develop in acropetal chains e.g. *Ramularia* spp. and some *Cladosporium* spp. the first formed conidia are more frequently septate than those formed later. In *Septonema secedens*, however, the conidia in the long chains are invariably 3-septate.

In 1951 Hughes (54) described three species of *Hansfordiella*, two of which produce phragmospores, the third dictyospores; other characteristic features seemed to demand their generic identity.

In *Stigmina platani* (Fuckel) Sacc. the conidia are apparently always phragmospores whereas in the single collection that I have seen of *S. platani-racemosae* (Dearn. & Barth.) Hughes 50% of the conidia are dictyospores; the two species only differ on this score and it seemed wrong to me to include the two in different genera to say nothing of different groupings (Hughes (66)).

The 'Helicosporae' seems to me to be the only Saccardoan grouping based on characters of mature conidia which classifies together species most of which have a similar type of conidium development.

In the primary division of Hyphomycetes into the two groups Xerosporae and Gloiosporae (Wakefield and Bisby (112) and Mason (83)) the presence or absence of slime around the conidia was held to be the distinguishing feature; but here again totally different types of conidia, with regard to their precise mode of development, are classified together and similar types widely separated. According to Ingold (70) a third 'biological spore type must be recognized, namely the aquatic spore produced, liberated and normally dispersed below water'; it was not suggested by this author that the aquatic spore types should comprise a third division of the Hyphomycetes. 'Biological spore type' is the correct appellation for dry, slimy, and aquatic spores; in addition 'biological conidiophore types' could be differentiated and even 'biological mycelium types'. Biological types can be overstressed; in the above instances they bear no relation to the more stable developmental and morphological characters of the reproductive structures. A large number of species do not fit adequately into either Xerosporae or Gloiosporae and may even change their position in either group according to the age of the fruiting structure. Under this scheme *Memnoniella* and *Stachybotrys* are widely separated whereas if the two genera were included under the one name,

Stachybotrys, no hardship would be suffered. As pointed out by Wakefield and Bisby (112) 'Also, of course, Nature presents us with the expected intermediate forms'. Mason (83) had already pointed out 'there is such an obvious transition between genera characterised by slimy phialospores to other genera characterised by dry phialospores'; I fail to understand, therefore, why 'moist spores verus dry spores' was made the 'primary differentiating character' in the List of British Hyphomycetes (Wakefield and Bisby (112)).

If the above mentioned characters are not regarded as important for the differentiation of major groupings of Hyphomycetes what then remains? The answer appears to me to be found at the apex (or the base!) of the conidiophore or sporogenous cell, or where the conidium initial is being produced. I believe that there are only a limited number of methods whereby conidia can develop from other cells and that morphologically related imperfect states will only be brought together when the precise methods of conidium origin take first place in the delimitation of the major groupings.

In the sections differentiated below, I have almost restricted myself to the commoner Hyphomycetes which I have collected on wood and bark in Britain; but a number of species from tropical Africa and North America have been included here and there in order to illustrate certain points. A few Coelomycetes have also been brought into the discussion.

The work of Vuillemin has been fully discussed by Mason (82, 83) who also proposed terms for types of 'conidia'. In Sections I to VIII (pp. 582-645) and in the very brief summary below, the term conidium is used throughout, except in Section IV in which phialospores develop from phialides (used in a restricted sense). Following the main text some of the terms of Vuillemin and Mason are discussed (pp. 647-650) and applied to the 'conidia' of the various sections where applicable. Langeron (76) used the terminology of Vuillemin and Mason but occasionally in so wide a sense that I believe some of the terms thus employed lost their usefulness.

Summary of Sections I to VIII

Growth of Conidiophore Initial or of Conidiophore During Sporulation Restricted to Apical Region

Section IA

Mycelium generally narrow. Conidia usually developing in acropetal succession as blown-out ends at the apex of simple or branched conidiophores which do not then increase in length. The basal conidia of chains aggregated around the apical region of a conidiophore may be morphologically different from the others and in one instance are modified into permanent metulae bearing a terminal conidium and a number of subterminal conidia.

Section IB

Mycelium generally wide. Conidia developing in acropetal succession as blown-out ends on simple or branched conidiophores; sometimes the lateral

branches are modified entirely into a number of conidia or into solitary conidia and in these instances the conidia are borne on conspicuous denticles. The solitary conidia or short, simple, or branched chains of conidia may be aggregated on well differentiated swollen cells and arise more or less simultaneously on them. In examples with intercalary or lateral swollen and fertile cells bearing simultaneously produced conidia, the main stalk may proliferate to develop further intercalary fertile cells or bear further lateral fertile branches.

Section II

Conidia arising as blown-out ends of apex of simple or branched conidiophores and the ends of successively produced new growing points developing to one side of the previous conidium. The conidiophore, therefore, either increases in length or becomes swollen as a result of conidium production. Acropetal chains of conidia may develop on the primary conidia.

Section III

Conidia usually thick-walled, arising solitarily as blown-out ends of apex of simple or branched conidiophores; a plurality of conidia may be produced, each new conidium developing as a blown-out end of successive proliferations *through* the scars of previous conidia so that the conidiophores in such cases become annellate.

Section IV

Conidia (phialospores) developing in rapidly maturing basipetal series from the apex of a conidiophore (phialide) which may or may not possess an evident collarette.

Section V

Conidia developing in gradually maturing basipetal series and originating by the meristematic growth of the apical region of the conidiophore in such a way that the chain of conidia merges imperceptibly with the conidiophore that gives rise to the chain.

Section VI

Conidia usually thick-walled, developing from pores on conidiophores of determinate or indeterminate length; they are solitary or in whorls, and may occur in acropetal chains. The conidiophore may proliferate through the terminal pore to produce a further terminal conidium or the conidiophore may develop a succession of terminal conidia on successive proliferations developing just below the previous conidium.

Section VII

Conidia developing by the basipetal fragmentation of conidiophores of determinate length, and which do not possess a meristematic zone.

Growth of Conidiophore Restricted to Basal Region

SECTION VIII

Conidia borne singly at apex, or singly at apex and laterally, often in regular whorls on conidiophores showing basal elongation. Conidia often with longitudinal slit in wall but this character is by no means restricted to this Section.

Section IA

The mycelium is immersed or superficial, composed generally of narrow hyphae.

The conidiophores are very variable in the different species, their variation being best explained by reference to various examples included in this section. In *Xylohypha nigrescens* (Fr.) Mason (Fig. 1) the conidiophores are short and closely packed together; each usually bears a single, very long, rarely branched acropetal chain of brown amerospores and at maturity a sooty pustule is formed. In **Bispora antennata** (Pers. ex Fr.) Mason comb. nov.* (Fig. 2) the conidiophores are likewise short and crowded together, each producing a single, long, unbranched, acropetal chain of dark brown to almost black didymospores. In *Septonema hormiscium* Sacc. (Fig. 3) the conidiophores are scattered and little different from conidia; the conidiophores bear a single short unbranched acropetal chain of dark brown phragmospores developing at the apex. There is a tendency for acropetal chains of conidia to be unbranched or seldom branched only when the conidiophores are closely aggregated.

By the production of simple or branched chains a plurality of conidia may be developed on a single conidiophore and this is not accompanied by an increase in length of the conidiophore itself; as in the original conidium so each succeeding one in the acropetal chain is the blown-out end of the previous conidium and throughout such a chain there is direct continuity between the wall of each conidium. In Section IA the conidia of all species develop as blown-out ends; amerospores, didymospores, and phragmospores are found here but as far as I am aware no dictyospores or staurospores develop in chains in acropetal succession.

In *Septonema solidum* Berk. & Curt. (≡ *Sirodesmium solidum* (Berk. & Curt.) Sacc.) 'conidia' develop from the apical growth of two to five dark brown and closely adpressed hyphae which develop constrictions at intervals at the same level thus giving the appearance of dictyospores in chains. The 'conidia' do not secede readily.

Septonema secedens Corda (Fig. 4), the type species of *Septonema*, is a form-species of great interest and helps to explain the relationship of a number of forms included in Section I; it has the advantage of enabling unbroken preparations to be made readily from young colonies, a single fructification is

* ≡ *Monilia antennata Pers. in Syn. Meth. Fung. p. 694. Gottingen. 1801.*
≡ *Torula antennata* [(*Pers.*)] *Pers. in Mycologia Europaea, 1 : 21. 1822.*
≡ *Torula antennata* [(*Pers.*)] *Pers. ex Fr. in Systema Mycologicum, 3 : 501. 1832.*
= *Bispora monilioides Corda in Icones Fungorum, 1 : 9. 1837.*

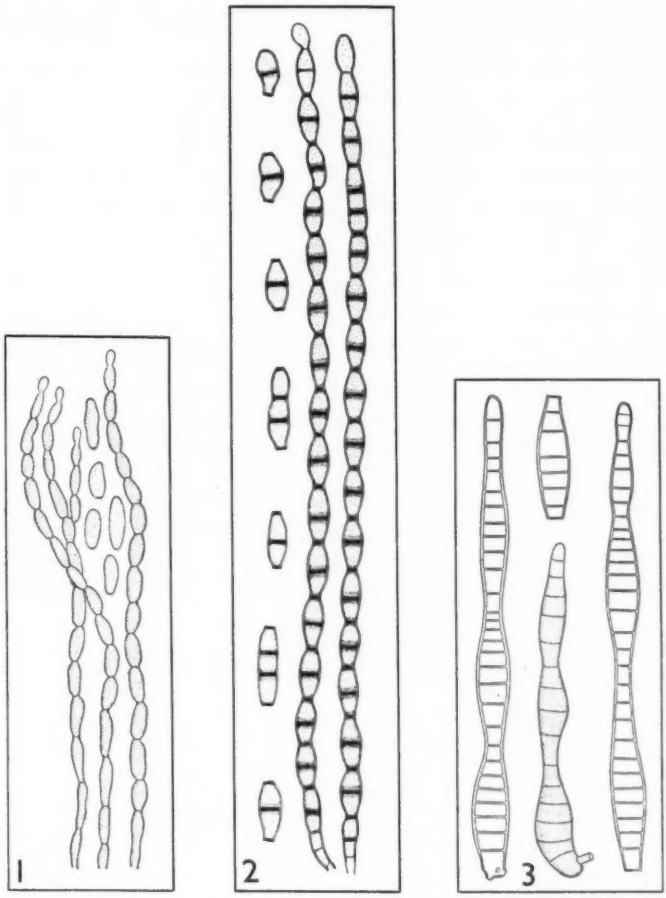


FIG. 1. *Xylohypha nigrescens*, isolated conidiophores with conidial chains, and conidia (I.M.I. 462); × 500.

FIG. 2. *Bispora antennata*, isolated conidiophores with conidial chains, and conidia (I.M.I. 9882); × 500.

FIG. 3. *Septonema hormiscium*, conidiophores and conidia from Hughes (61); × 500.

large and the whole development and sequence of events can easily be followed obtained. The main stalk of the conidiophore, therefore, has resolved itself (Hughes (56)). The conidiophore is formed from an upturned repent hypha or from an erect lateral branch; it is up to 200μ long, 4-5μ wide*, septate, and with the septa 18-25μ apart. Towards the apex of the mature conidiophore, constrictions are found at the septa in increasing depth and with the

* *All measurements given in this paper were made from preparations in lactic acid, with or without cotton blue.*

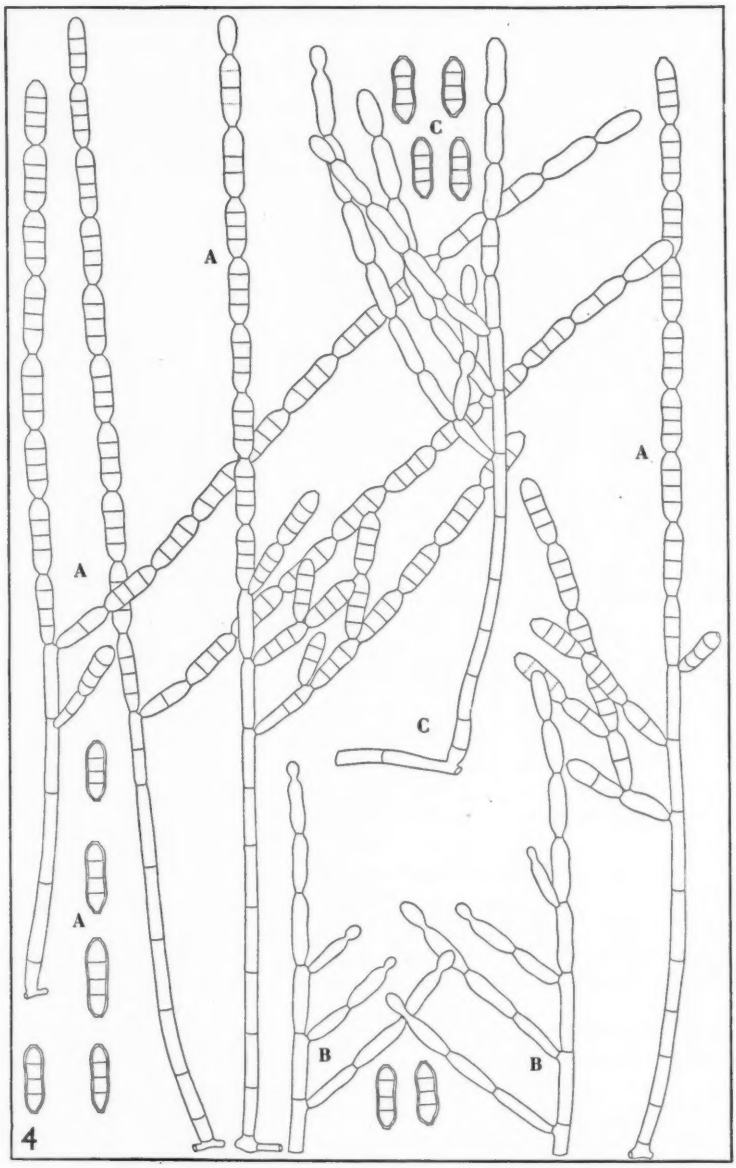
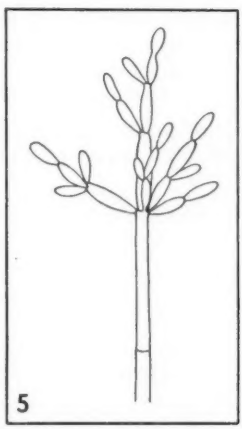


FIG. 4. *Septonema secedens*, conidiophores and conidia from Hughes (56); × 500.

slightly wider cells formed in acropetal succession a long-beaded effect is above, by acropetal growth, into a chain of conidium initials separated by septa at constrictions. Towards the apex of the conidiophore, at different levels, up to four lateral acropetal branches develop; and at the septa of the branches constrictions occur from their first formation, and these may also bear secondary and then even tertiary lateral branches; all the cells of the lateral branches are conidium initials (18-23μ long) and a more or less arborescent (albeit occasionally unilateral) appearance is the result. The mature conidiophore and chains of conidia in *Septonema secedens* is merely a branched aerial hypha, the laterals and the upper part of the main stalk of which have developed as conidial units. Maturity in this fungus is reached with the development of color and of three septa in each initial although the basal conidia of the terminal and lateral chains may be only once or twice septate or even continuous.

In **Septonema harknessii** (Ellis) comb. nov.* the fructification is exactly like that of *S. secedens* but the conidia are much larger and up to 7-septate at maturity. In **Septonema leptaleum** (Ellis) comb. nov.** the conidia are up to 7-septate but narrower than those of *S. harknessii*.

In a young development of *Septonema secedens* (Fig. 4, *B*, *C*) the appearance of the conidiophore and chains is very reminiscent of the *Cladosporium*-type of conidial apparatus (Fig. 5) produced by '*Ceratostomella pluriannulata*' (Lagerberg, Lundberg, and Melin (75)) where all the conidia are amerospores



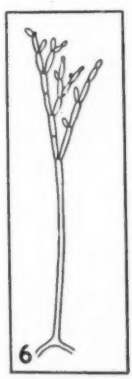
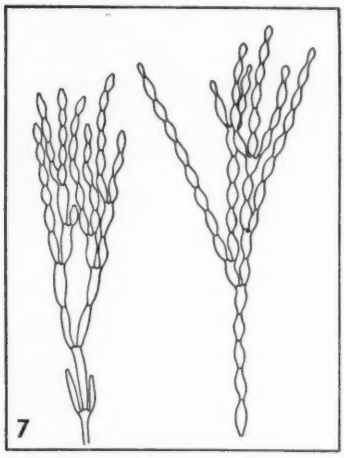


FIG. 5. '*Ceratostomella pluriannulata*', conidiophore and conidia from Lagerberg, Lundberg, and Melin (75); × 910.

FIG. 6. *Cladosporium* sp., conidiophore and conidia from Brett (14); slighty reduced from original.

* ≡ *Dendryphion harknessii Ellis in Bull. Torrey Botan. Club, 8 : 27. 1881 (as Deudryphium).*
** ≡ *Dendryphion harknessii var. leptaleum Ellis in Bull. Torrey Botan. Club, 8 : 27. 1881 (as Dendryphium).*
≡ *Dendryphion leptaleum (Ellis) Sacc. in Sylloge Fungorum, 15 : 112. 1901 (as Dendryphium leptaleum Ell.).*



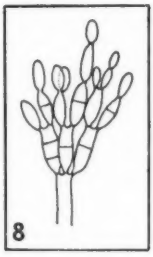


FIG. 7. *Cladosporium harknessii*, portion of conidiophore and two branched chains of conidia (DAOM 28997); × 475.
FIG. 8. *Cladosporium* sp., apex of conidiophore and conidia from Bisby (9); × 450.

and again where the development of conidial chains is the same. A similar '*Cladosporium*'-type of fructification (Fig. 6), illustrated by Brett (14) was this conidiophore bears unilateral branches as is so often found in *Septonema secedens*.

In **Cladosporium harknessii** (Peck) comb. nov.† (Fig. 7) the fructifications are compact and brownish; the tremendously long, branched, acropetal chains are composed of more or less lemon-shaped amerospores. Towards the base of the chains the conidia are longer, almost cylindrical, and merge gradually with the thin, branched conidiophores below as they do with the shorter conidia above. Peck† stated that this species is 'related to and congeneric with such species as *Oidium aureum*. . . .' !

In one of Bisby's (9) illustrations of a Canadian isolation of *Cladosporium* sp. (Fig. 8) the lower conidia in the branched system are variously septate but they secede as readily as the others and function as conidia. These lower conidia in the chain have been called 'ramoconidia' by Mr. Mason (oral communications) and although the term is not restrictive its does imply that the lower or first formed conidia are somewhat different from the smaller upper ones formed later. Differences in the component conidia of acropetal chains are not at all uncommon especially in *Ramularia* spp. (e.g. *R. onobrychidis* Allesch. (Hughes (43)) and *Septonema pallidum* (Grove) Hughes (61).

Dendryphion griseum Berk. & Br. seems to be somewhat half way between *Cladosporium* and *Septonema*. In this fungus (Fig. 9) the conidiophore is of determinate length and one to three branched chains of conidia are produced on short denticles at the apex. The conidia are continuous to 3-septate whereas in *Septonema* the conidia are mostly three or more septate at maturity. And this seems to me to be the only real difference between the two genera

† = *Monilia harknessii Peck in N.Y. State Museum Rept., 34 : 49. 1883 [as 1881].*

although it must be admitted that *S. secedens* and *S. harknessii* do not remind one much of a *Cladosporium*. *Dendryphion griseum* in any case is not a *Dendryphion* and I consider it to be best classified as **Cladosporium griseum** (Berk. & Br.) comb. nov.*

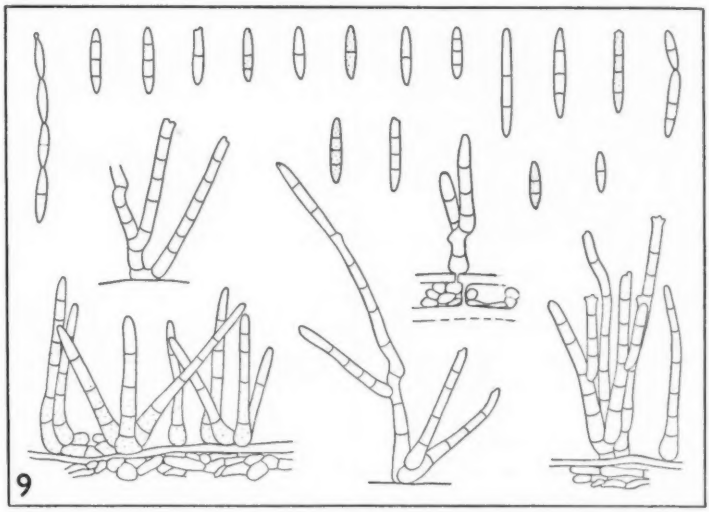
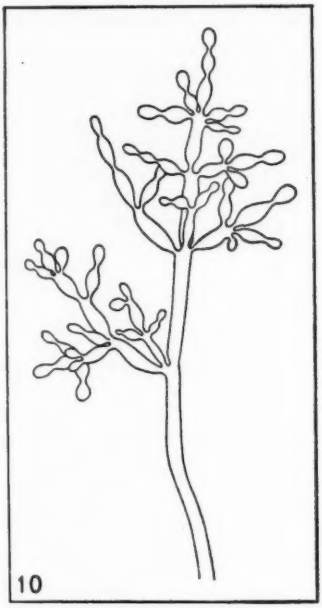


FIG. 9. *Cladosporium griseum*, mycelium, conidiophores, and conidia (I.M.I. 4333); × 500.

De Vries (30) has discussed conidium development in *Cladosporium* spp.; his figure of *C. avellaneum* de Vries forma *avellaneum* de Vries is reproduced here as Fig. 10. In *C. cladosporioides* (Fres.) de Vries he figured the conidiophores as not increasing in length whereas in *Heterosporium variabile* Cooke (which he called *Cladosporium variabile* (Cooke) de Vries) the main stalk of the conidiophore was shown to increase in length by the development of a succession of lateral subterminal growing points and terminal conidia produced in turn at each new growing point after varying degrees of elongation; chains of conidia produced on the primary conidia, however, develop in the manner of *Cladosporium* proper. (A similar type of conidiophore elongation and production of *Cladosporium*-like chains is found on the primary conidia of *Ramularia* spp. e.g. *R. onobrychidis* Allesch.). This character of the increase in length of the main stalk of the conidiophore in some species, or of sporogenous cells in other species, I consider to be of paramount importance in the classification of Fungi Imperfecti as set out here. (This type of development is dealt with in Section II and will include such fungi as *Helminthosporium* auct (e.g. *H. apiculatum*), *Heterosporium*, *Dactylosporium*, *Atractina*, and *Tritirachium* to mention only a few.)

* = *Dendryphion griseum Berk. & Br. in Ann. Mag. Nat. Hist. II, 7 : 177. 1851* [*as Dendryphium*].



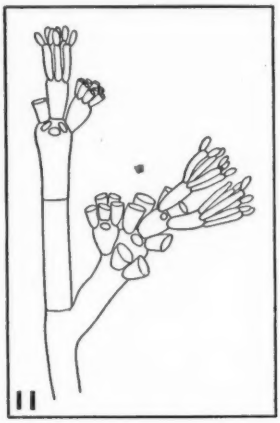


FIG. 10. *Cladosporium avellaneum* forma *avellaneum*, conidiophore and conidia from de Vries (30); slightly reduced from original.

FIG. 11. *Hyaloscypha dematiicola*, part drawing of conidiophore with metulae and conidia from pure culture (DAOM 28286(*b*)); ×1000.

In *Haplographium delicatum* Berk. & Br. (= *H. bicolor* Grove)* (Fig. 11), the type species of *Haplographium* Berk. & Br., I consider that a much modified and very condensed *Cladosporium*-type of conidiophore fructification occurs. The conidiophores of *Hyaloscypha dematiicola* are erect, simple, septate, thick-walled, and brown except at the paler apex and it is altogether a well differentiated structure. At maturity the apex is capped by a ball of slime containing conidia and partially enveloping the other cells upon which they were borne. In pure culture on malt agar the solitary globules of conidia are about 35 μ in diameter and very occasionally up to 45 μ. When neighboring conidial globules touch they unite, with the result that often an extensive sheet of slimy conidia can be formed. Around the apex of the main stalk are borne up to eight oval, pale brown metulae surrounding a central metula which is really a continuation of the growth of the main stalk. Each primary metula bears secondary metulae in the same way that the apex of the main stalk of

* *I have shown by pure cultures in Britain that Hyaloscypha dematiicola (Berk. & Br.) Nannfeldt (det. R. W. G. Dennis) is the perfect state of this Haplographium. Both states were found frequently together in Britain (as they are on the type!) and I also find the same association in my collections of this fungus in New York State, U.S., and Ontario, Canada. It has received one independent name in Canada:*

= *Scopularia populi Dearn. & Bisby apud Bisby et al. The Fungi of Manitoba. 1929, p. 130.*

the conidiophore bears primary metulae but the secondary metulae are narrower and usually hyaline to subhyaline. Similarly, tertiary metulae (in a perfectly formed head) are borne on the secondary ones; these are hyaline and narrower than the secondary metulae. There can be differentiated, therefore, three rows of metulae which are successively narrower, proceeding distally from the apex of the main stalk of the conidiophore. Each tertiary metula bears an apical conidium produced as a blown-out end (as are the metulae themselves) and three or four lateral and subterminal conidia have been seen attached although perhaps more than this may develop. I have seen no chains of conidia. As detected by their smaller dimensions conidia may be seen to have developed on some secondary metulae in place of one or more tertiary metulae. In depauperate conidiophores even the secondary metulae may be replaced by conidia. The slimy head of this *Haplographium* conidiophore I consider therefore to be homologous with a *Cladosporium* conidiophore but with a more well differentiated conidiophore and condensed and regularly whorled lateral branches; furthermore the crowded primary and secondary branches (metulae) have developed into permanent structures, failing to secede at maturity. The primary and secondary metulae may be considered, paradoxically, to be 'ramo-conidia' which do not secede and which can more obviously be differentiated from the conidia than can the ramo-conidia of *Cladosporium* from the other conidia in the *Cladosporium* chains. In *Hyaloscypha dematiicola* the tertiary metulae may become detached from the secondary metulae and function as conidia but they may be differentiated by their larger size.

Abnormalities in the head of conidial *Hyaloscypha dematiicola* are not uncommon in field collections or pure culture on agar media. Perhaps the most interesting ones are those in which the central primary metula is much longer than the lateral ones thus more obviously indicating the nature of the central metula as being a continuation of the growth of the conidiophore. The central tertiary metula may even bear quaternary metulae. Then again one of the lateral primary metulae may appear as a brown cylindrical cell, larger than the other metulae and resembling a side branch of the conidiophore; like the main stalk this enlarged metula bears a slimy head of metulae and conidia.

It has been claimed (Mason (82)) that the conidia in this fungus are abstricted from the sporophores in immense numbers but I am unable to verify this. In pure culture where development can be observed more easily the slimy head of conidia is more or less hemispherical on the compact branched head of the main stalk of the conidiophore. In a slimy head 40μ in diameter I calculate that there are about 2500 conidia (measuring $3.5 \times 1.5\mu$); this approximates the number which would be borne in a regular head composed of a succession of nine primary, eight secondary, and seven tertiary metulae bearing five apical and subapical conidia.

Section IB

In Section IB are classified species some of which have a striking morphological similarity with some forms included in Section IA. Now in IA the mycelium is for the most part composed of narrow hyphae whereas in Section IB the hyphae and conidiophores are wide and these often form a superficial weft on natural substrata. In most of the forms included here the conidia develop on specialized terminal or intercalary swellings of the main stalk of the conidiophore or on terminal swellings of lateral branches.

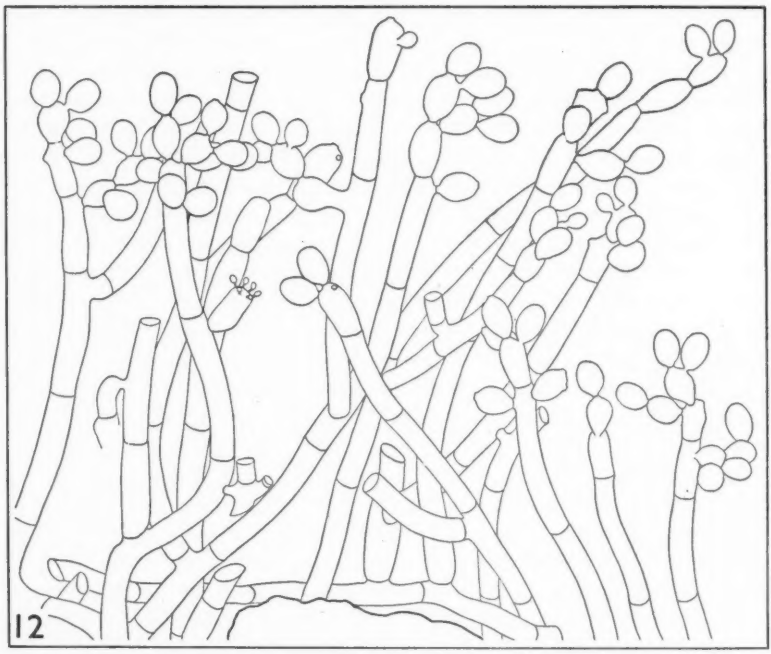
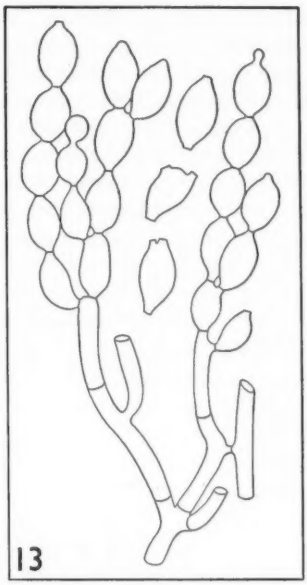


FIG. 12. *Pellicularia pruinata*, conidiophores (one of which bears a basidium), and conidia from Hughes (50); ×500.

In *Pellicularia pruinata* (Bres.) Rogers (Fig. 12) (Hughes (50)) the sparingly branched conidiophores are really of the *Cladosporium*-type (Fig. 10); the long, erect, and wide conidiophores are modified above into a terminal acropetal chain of more or less oval conidia which are denticulate at both ends whilst the lateral branches are also modified into conidia, entirely or for most of their length. In *Oidium aureum* Link ex Fr. (Fig. 13), the type species of the genus, a similar state of affairs is found but the shorter conidiophores are themselves more branched towards the base; they bear a terminal acropetal chain of conidia and lateral ones as well.

The morphology of *Torula ramosa* Fuckel (Fig. 14) is immediately reminiscent of *Oidium aureum* although the dematiaceous nature of the mycelium,



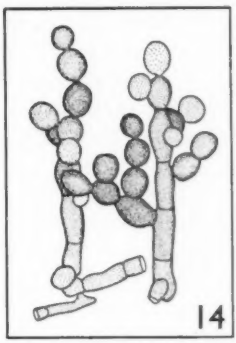


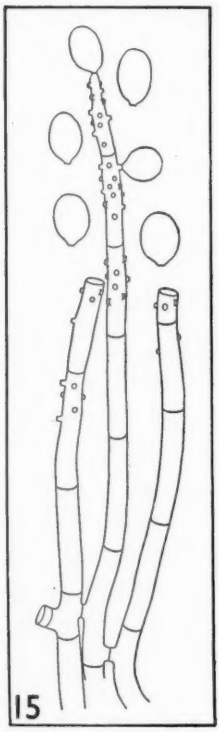
FIG. 13. *Oidium aureum*, conidiophores and conidia (I.M.I. 5366); ×500.
FIG. 14. *Oidium ramosum*, mycelium, conidiophores, and conidia (I.M.I. 6072); ×500.

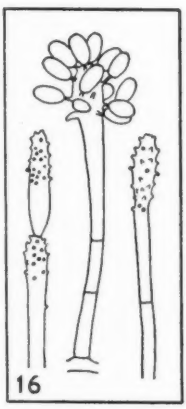
conidiophores, and conidia does not really fit the fungus for adequate inclusion in the genus *Oidium*; Linder (78) stated that in *Oidium* the conidiophores are never black or fuscous. Another species in Herb. I.M.I. is congeneric with *Torula ramosa* and together these two black molds may well constitute a new genus. At present, however, I prefer to dispose those collections in Herb. DAOM as **Oidium ramosum** (Fuckel) comb. nov.*

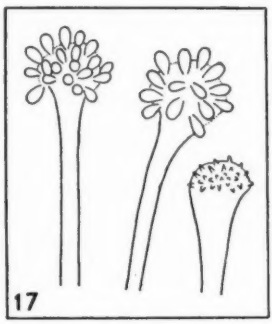
In Linder's treatment of the genus *Oidium* Link ex Fr. there seems to be two main groups of species, (1) those in which the conidiophores (often merely repent hyphae) produce vesicles bearing solitary conidia or chains of conidia on denticles or conidiophores with chains of conidia produced directly upon them, and (2) those in which the conidiophores bear a number of conidia solitarily on conspicuous denticles which are not usually restricted to any one cell of the conidiophore and those cells bearing the denticles are not at all or only slightly swollen. (An odd species *Allescheriella crocea* (Mont.) Hughes (50) (= Linder (78) sub *Oidium simile*) (Fig. 46) I consider best classified in *Allescheriella* (Section III) of which generic name this is (as *A. uredinoides*) the type species).

* ≡ *Torula ramosa Fuckel in Symbolae Mycologicae, p. 348. 1870.*
= *Torula ramosa Peck in N.Y. State Museum Rept., 32 : 39. 1880 [as 1879].*
≡ *Torula peckii Sacc. & Syd. in Sylloge Fungorum, 14 : 1070. 1899.*
The type collections of both names have been seen; the former at Herb. R.B.G. Kew, England, and the latter at New York State Museum, Albany, N.Y. A recent collection from Canada is DAOM 28726, on wood, Merivale Woods, near Ottawa, Ont., 24.vii.1952.

Some 22 species treated by Linder, including *Pellicularia pruinata* (= *Oidium candicans* (Sacc) Linder) and *Oidium aureum* are found in the first group and amongst themselves show a great deal of variation. In *Pellicularia pruinata*, for instance, some lateral conidial branches are composed of only a single conidium borne on a denticle although most lateral branches are two or three conidia long. There is no clear line separating the two groups. In *Oidium conspersum* (Link) Linder (Fig. 15), the type species of the generic name *Acladium* Link, which would be included in the second group of species the erect conidiophores are terminated by a single conidium and along the upper three quarters of the length of the septate conidiophores are borne solitary conidia on well marked denticles; five other species included by Linder are similar to *O. conspersum* in this way. In *O. conspersum* I have not observed any particular regular order in the production of the conidia other than a more or less simultaneous development or a haphazard one. I agree with







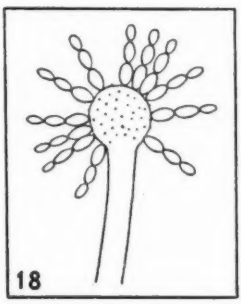


FIG. 15. *Oidium conspersum*, conidiophores and conidia (I.M.I. 15528); ×500.
FIG. 16. *Oidium tenellum*, conidiophores and conidia from Linder (78); ×255.
FIG. 17. *Fomes annosus*, conidiophores and conidia from Bakshi (5); ×777.
FIG. 18. *Nematogonium parasiticum*, apex of conidiophore, and conidia from Thaxter (110) sub *Gonatorrhodiella parasitica*; ×281.

Linder that *O. conspersum* and the similar species are best classified along with *O. aureum*, the type species, even though the conidia are solitary or, as I prefer to look upon it and paradoxical though it may seem, even though the lateral chains of conidia have been reduced to single conidia. In *Oidium* spp., those with chains of conidia have few lateral (conidial) branches whereas in those species producing solitary terminal and lateral conidia the conidiophores bear numerous denticles supporting such solitary conidia.

If one now considers *Oidium tenellum* (Berk. & Curt.) Linder (Fig. 16) it will be observed that the denticles bearing solitary conidia are numerous and are restricted to the upper regions of one, two, or three terminal cells of the conidiophore; furthermore, these cells are slightly swollen and immediately suggest the conidial apparatus found in *Oedocephalum* (e.g. *Fomes annosus* (Fr.) Cooke, Fig. 17) and a number of other genera whose members have conidia produced on denticles on swollen cells of the conidiophore or its lateral branches. *Oidium tenellum* certainly seems to provide a connecting link between such species as *O. conspersum* and those with the *Botrytis–Oedocephalum* type of fructification. Such genera are briefly mentioned below but it is worth while drawing attention to the fact that *Gonatobotryum fuscum*, *G. apiculatum* (see p. 594), *Nematogonium parasiticum* (see p. 594) and others produce chains of conidia on denticles. In *Gonatobotryum apiculatum* the short chains are seldom branched whilst in *Nematogonium aurantiacum* the chains of conidia, which are characteristically smaller towards the apex of a chain, are always branched.

Oedocephalum spp. are characterized by simple, erect conidiophores producing conidia more or less simultaneously on denticles on a swollen terminal cell (ampulla). Such conidiophores are produced by *Fomes annosus* (Fig. 17) (see Bakshi (5, 6) sub *Oedocephalum lineatum* Bakshi, and Olson (94) sub *Cunninghamella meineckella* Olson); this was observed in 1889 by Brefeld (13) who proposed the generic name *Heterobasidion* for the conidiophores. Brefeld figured a number of conidiophores with lateral branches arising from the terminal ampulla. An *Oedocephalum* conidial apparatus has been reported also for '*Pyronema omphalodes* (Bull.) Fuckel' by a number of authors, e.g. Schmidt (102). *Oedocephalum echinulatum* Thaxter (109) has minutely echinulate conidia; in this publication Thaxter altogether described four species of *Oedocephalum* including *O. verticillatum* Thaxt., an interesting form with verticillate branches bearing terminal, conidium-bearing, denticulate ampullae.

In *Rhopalomyces elegans* Corda a simple conidiophore bears a terminal ampulla bearing colored conidia. Thaxter (109) beautifully illustrated this fungus and also described and illustrated another species *R. strangulatus* Thaxt. Boedijn (11) considered *R. elegans* to be one of the Mucorales.

In *Gonatobotrys simplex* Corda a simple hyaline conidiophore bears a terminal and a number of intercalary ampullae, each roughened by conidium-bearing denticles; the conidia are hyaline and continuous. The fungus was illustrated by Corda (24) and Drechsler (33).

In *Gonatobotryum fuscum* Sacc. a simple, pale brown conidiophore has the same form as that of the preceding species; the conidia are oval, pale brown, and are borne in chains of two.

In **Gonatobotryum apiculatum** (Peck) comb. nov.* the conidiophores are simple, erect, dark brown with terminal and intercalary ampullae bearing crowded conidia on denticles. The conidia are borne in short, seldom branched chains. The fungus is found on leaf spots of *Hamamelis* in North America and has been figured by Overholts (96) (as *G. maculicola*).

Nematogonium aurantiacum belongs in Section IB; it produces orange colored colonies. The conidiophores have terminal and intercalary ampullae which produce short branched chains of conidia on denticles, the distal conidia being successively smaller. Ayers (3) has described and figured a fungus associated with *Nectria coccinea* (Pers. ex Fr.) Fr. on *Fagus grandifolia* as *Gonatorrhodiella highlei* A. L. Smith (105) (e.g. Reliquiae Farlowianae 998 on *Nectria coccinea* on *Fagus*, Maine, U.S., det. Ayers as *G. highlei*). The fungus in this collection is identical with de Thümen, Mycotheca universalis 1665 on *Platanus occidentalis* in socio *Nectria* sp., France, sub *Nematogonium aurantiacum* Desm., and with Ellis and Everhart, Fungi columbiani 372 on *Magnolia glauca* in socio ?nectriaceous fungus, New Jersey, U.S., sub *Nematogonium aurantiacum*. It seems highly probable to me that the fungus assigned to *Gonatorrhodiella highlei* in North America is *Nematogonium aurantiacum*.

Gonatorrhodiella parasitica Thaxter† (110), the type species of this genus, was described as apparently parasitic on *Hypocrea* and *Hypomyces* from Connecticut; it has hyaline conidiophores which later become pale fawn being simple or sparingly branched, bearing apical and intercalary ampullae. The conidia are borne on denticles, which are crowded on the ampullae, and are in chains of three, the distal conidia being somewhat smaller than the proximal ones (Fig. 18). In its habit of being a consociant of other fungi, its morphology, and the color of mycelium, conidiophores, and conidia, *Gonatorrhodiella parasitica* does not appear to me to be generically distinct from *Nematogonium*; the following new combination is therefore proposed: **Nematogonium parasiticum** (Thaxter) comb. nov.

In *Mycotypha microspora* Fenner (36) the conidiophores have the apex swollen into a cylindrical ampulla; the continuous hyaline conidia are closely packed, being borne solitarily on denticles. Martin (81) considered this fungus to be one of the Mucoraceae and as such was it described by Fenner.

In *Blastophorella* Boedijn (12), based on *B. smithii* Boed., the conidiophore is swollen into a cylindrical ampulla as in *Mycotypha* but the conidia are oval and 1-septate.

* ≡ *Haplographium apiculatum Peck in N.Y. State Museum Rept., 28 : 62. 1876 [as 1875].*
= *Gonatobotrys maculicola Wint. in Bull. Torrey Botan. Club, 10 : 7. 1883 (Jan.).*
≡ *Gonatobotryum maculicola (Wint.) Sacc. in Sylloge Fungorum, 4 : 278. 1886.*

† = *Gonatobotrys lateritia Peck in N.Y. State Museum Bull. 131 : 21. 1909. Peck described his species on Poria sp. on Platanus from Star Lake, St. Lawrence Co., N.Y., U.S.*

Sigmoideomyces dispiroides Thaxter (109), the type species of the genus, and *S. divaricatus* McLean (79) produce conidia on denticles on spherical ampullae which are borne on well differentiated enveloping hyphae.

The botryose clusters of conidia in *Botrytis* spp. are well known and it is to the conidium-bearing swellings of *Botrytis* that the term 'ampullae' was first applied (by Klebahn (74) fide Whetzel & Drayton (114) who used it for *Botrytis convoluta* Whetz. & Drayt.). The term ampulla has been used here in Section IB for the terminal and intercalary swellings bearing conidia which are usually on denticles and which arise more or less simultaneously. In 1887 de Bary (28) drew attention to the simultaneous origin of conidia in *Sclerotinia fuckeliana* (*Botrytis cinerea* Pers. ex Fr.). (Mason (82) first used the term 'radula spores' for the conidia borne all over the surface of the ascospores of *Nectria coryli* Fuckel whilst still within the ascus; but because these spores may be 'the homologues of the usual phialospores' the term radula spores cannot be used for the conidia of the *Botrytis* type of fungus. Later in the same publication, however, Mason used the term for the *Botrytis* conidia which were described as developing without any reference to a growing point. If the conidia of *Nectria coryli* are phialospores then the term radula spore may refer to conidia which are not precisely homologous. In 1937 Mason (82) returned to the subject of radula spores and differentiated the *Nectria coryli* type as 'slimy radula spores' from the 'dry radula spores' of *Botrytis*. Nannfeldt (in Melin and Nannfeldt (87)) used 'radula spores' for the conidia of *Rhinocladiella atrovirens* Nannf. but I find that in this fungus they arise not more or less simultaneously, or without reference to a growing point, but successively as the blown-out ends of successively produced growing points. For these reasons the confused term 'radula spore' is not here applied to the *Botrytis* type of conidium.)

Botrytis conidiophores are produced by *Sclerotinia draytoni* Budd. & Wakef. (Dennis & Wakefield (29)), *S. spermophila* Noble (91), *S. polyblastis* Greg., *S. narcissicola* Greg., and *S. sphaerosperma* Greg. (Gregory (40)) and *Sclerotinia fuckeliana* de Bary (*Botryotinia fuckeliana* (de Bary) Whetz.) which is known generally in its conidial state as *Botrytis cinerea* Pers. ex Fr.

Elaborate ampullae are the conspicuous features of *Botryosporium* spp. *B. longibrachiatum* (Oud.) Maire is not uncommon in glasshouses in Britain whilst *B. pulchrum* Corda is found outdoors; the last named species is illustrated in Fig. 19. Each conidiophore is repeatedly dichotomous and bears the really striking lateral fertile branches.

Chaetosphaeria phaeostroma (Dur. & Mont.) Fuckel is the presumed perithecial state of *Cladotrichum triseptatum* Berk. & Br. and is not uncommon in Britain on old diatrypaceous fungi. The brown conidiophores mixed with concolorous setae form a shining velvety growth; the conidiophores (Fig. 20) are broad, dichotomously branched with intercalary and terminal more or less spherical ampullae upon which oval to oval-cylindric 3-septate conidia arise more or less simultaneously. *Chaetosphaeria fusca* Fuckel, another fungus which is a consociant of sphaeriaceous fungi, I have collected once in Britain

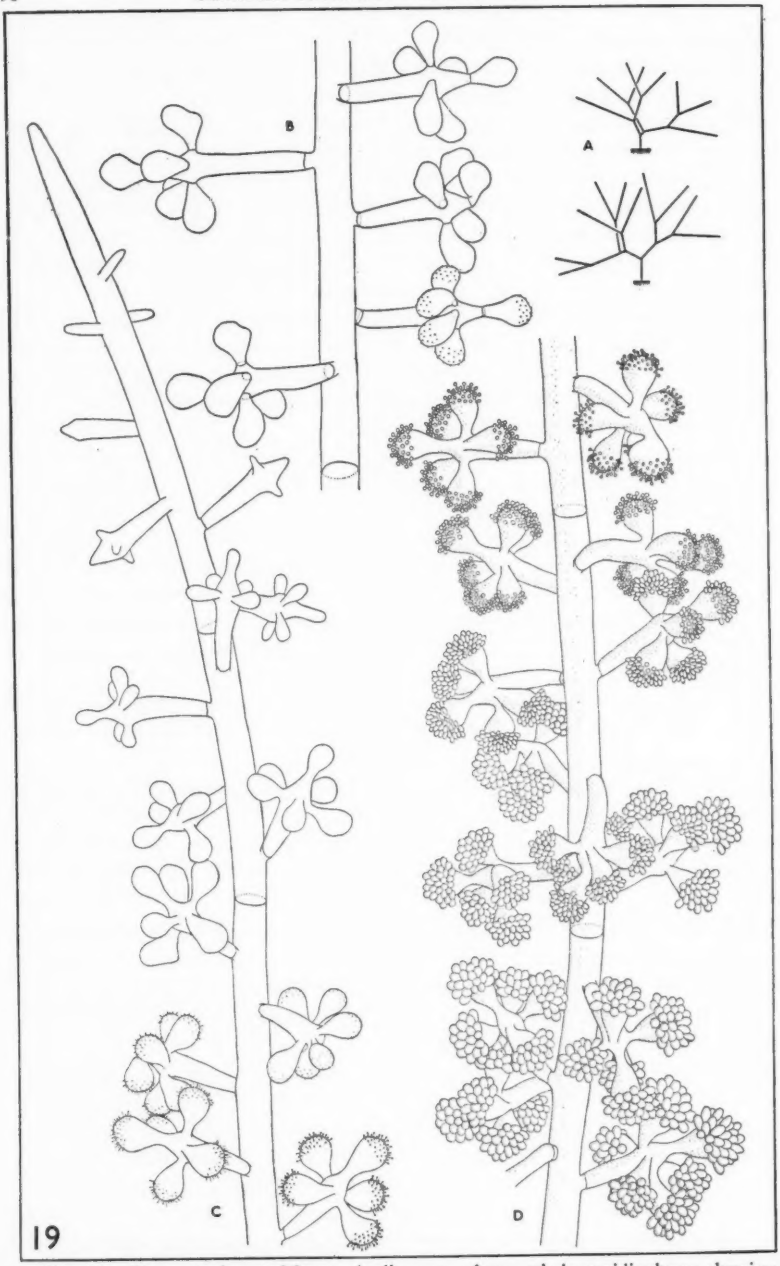


FIG. 19. *Botryosporium pulchrum*, *A*, diagrams of two whole conidiophores showing dichotomous branching; *B*, *C*, *D*, apical and intercalary portions of conidiophore branches, and conidia (I.M.I. 1359); *B*, *C*, *D*, ×500.

in its presumed conidial state (*Cladotrichum scythophorum* Corda). The sparingly branched and adpressed conidiophores have terminal and intercalary ampullae each bearing a few acropetal chains of waisted-oval, 1-septate conidia, the first conidia of each chain having arisen more or less simultaneously.

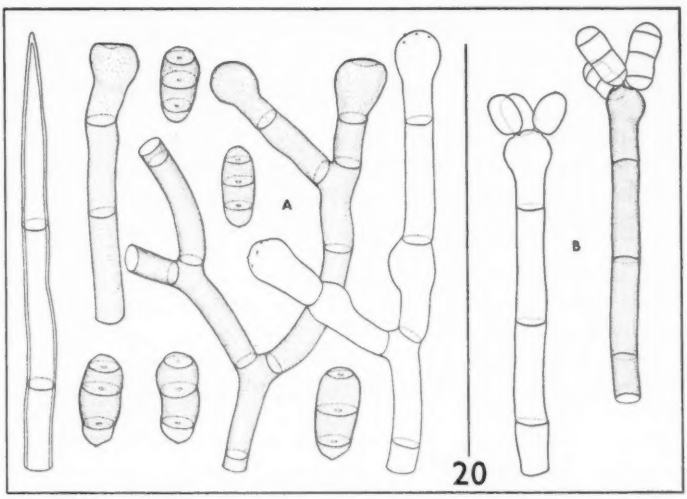


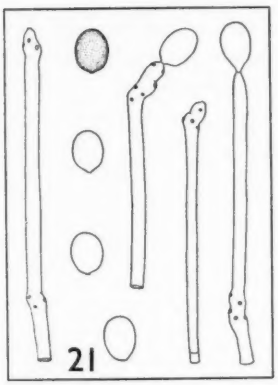
FIG. 20. *Chaetosphaeria phaeostroma*, mycelial seta, portions of conidiophores, and conidia; *A*, I.M.I. 1694; *B*, I.M.I. 1354; ×500.

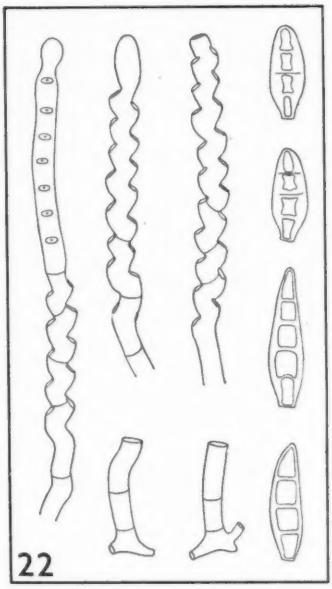
It is interesting to note that many of the conidial fructifications included in Section IB have been shown to be Basidiomycetes, Phycomycetes, Discomycetes, and Pyrenomycetes; furthermore it appears that they are all perfectly dry-spored.

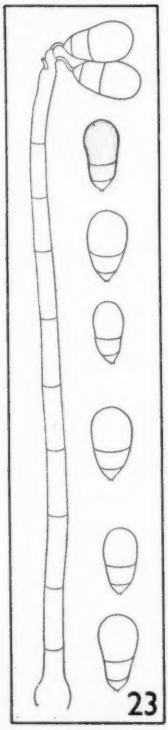
Section II

The mycelium is immersed or superficial, generally narrow but sometimes as wide as the conidiophores.

In this section the conidia are produced as blown-out ends singly at the apex of the conidiophore and of the successive new growing points which develop just to one side of the previous terminal conidium. At maturity, therefore, a conidiophore or sporogenous cell producing conidia in this way possesses a number of scars; each one of these was in turn terminal (during the development of the now fallen conidium) before being pushed aside by the development of a new growing point. Such conidiophores usually show a perceptible increase in length with the development of each conidium; but in some species a succession of conidia developing on a succession of growing points results not always in a longitudinal extension of the conidiophore or sporogenous cell but the apex becomes swollen with the development of successive conidia.







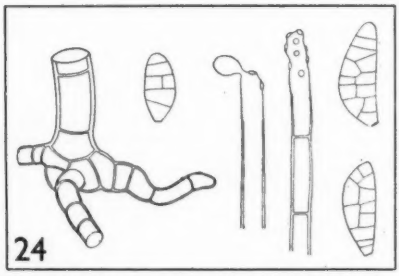


FIG. 21. *Virgariella atra*, apices of conidiophores, and conidia (I.M.I. 27613); ×500.
FIG. 22. *Helminthosporium guareicola*, conidiophores and conidia from Hughes (68); ×500.
FIG. 23. *Brachysporium obovatum*, conidiophore and conidia from Hughes (48); ×500.
FIG. 24. *Dactylosporium macropus*, portions of conidiophores and conidia from Hughes (63); ×500.

The distance between the successive scars is often fairly constant but in some species it varies considerably; this distance, of course, depends on the activity of the new growing point before blowing-out into a new terminal conidium. In *Virgariella atra* Hughes (Fig. 21; see also p. 654) groups of conidial scars along the length of the conidiophore alternate with smooth portions where there has been no conidium production; I have observed this in cultures of '*Acrothecium simplex* Berk. & Br.' and '*Acrotheca acuta* Grove'*, and also in *Helminthosporium guareicola* Stevens (Fig. 22) (Hughes (68)) and *Daldinia angolensis* (Welw. & Curr.) Sacc. (Hughes (59)). The interrupted conidium production is seen to best advantage in *Arthrobotrys* spp. e.g. *A. superba* Corda (Drechsler (32) and also Matruchot (86)), the resultant conidiophore having the appearance of one of the members of Section IB such as *Gonatobotrys simplex* Corda in which species the conidia on each ampulla arise simultaneously; in *Arthrobotrys* the swellings are the result of the successive development of closely inserted conidia.

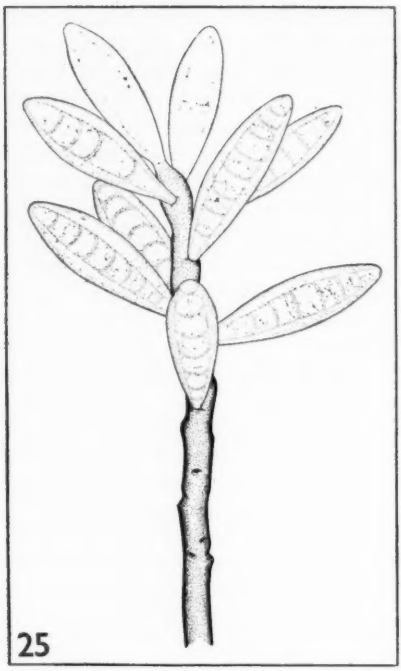
A further example is found in *Cordana* sp. I in Herb. DAOM in which a succession of conidia results in a swollen apex to the conidiophore, and furthermore with further growth sterile lengths of conidiophore may eventually alternate with fertile swellings. This is very reminiscent of the illustration by Sibilia (104) of *Arthrobotryella hernica* Sibilia; numerous phaeodidymospores are shown attached to denticles on well differentiated ampullae but I do not know whether the conidia arise in succession or simultaneously. Close observation of the *Echinobotryum* conidia of *Stysanus stemonitis* (Pers. ex Fr.) Corda indicates that these, too, arise in succession, on a short hypha the apex of which becomes swollen as further conidia develop.

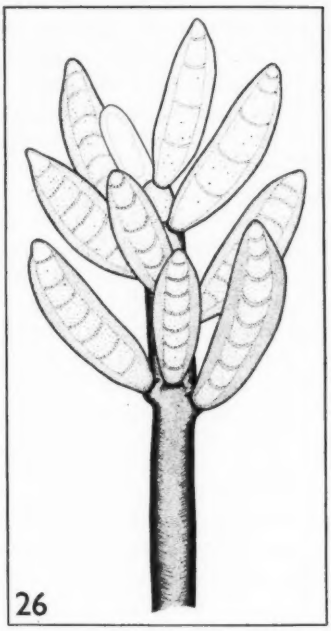
In some species e.g. *Brachysporium obovatum* (Berk.) Sacc. (Fig. 23) (Hughes (48)) and *Dactylosporium macropus* (Corda) Harz (Fig. 24) (Hughes (63)) the conidiophores are simple and more or less setose, being dark brown and thick-walled. In '*Helminthosporium simplex* Kunze' (Fig. 25) and '*H. apiculatum* Corda' (Fig. 26), two not uncommon molds of wood in Britain, dematiaceous fusoid conidia are formed successively; both species have been collected in North America. In *Diplorhinotrichum candidulum* v. Höhn. (Fig. 27) the conidiophores are generally short, thin-walled, and more or less hyaline.

In the foliicolous *Camptomeris* spp. (Hughes (66)) well differentiated conidiophores are unilaterally thickened and produced on specialized vesicular supporting-cells which are subglobose to cylindrical with somewhat inflated distal ends. In the *Polythrincium* conidiophores of *Cymadothea trifolii* (Pers.) Wolf (Hughes (66)) conidiophores are also produced on a palisade of cylindrical vesicular cells.

In *Cercospora* spp. the conidiophores are borne on an immersed or semi-immersed stroma and the genus is usually classified amongst the Dematieae. *Isariopsis griseola* Sacc. has almost synnematous conidiophores with conidia like those of *Cercospora* and is classified amongst the Stilbaceae. The genera

* *Acrotheca acuta Grove is completely out of place in Acrotheca (= Ramularia Unger fide Hughes (49)) and could, I believe, be adequately placed in the genus Rhinocladiella Nannf.*





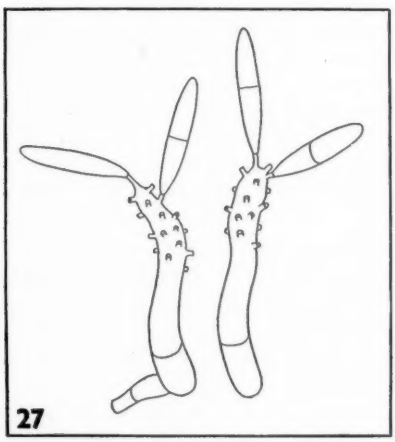


FIG. 25. *Helminthosporium simplex*, conidiophore and conidia (I.M.I. 1353); ×750.

FIG. 26. *Helminthosporium apiculatum*, conidiophore and conidia from pure culture (I.M.I. 1357); ×750.

FIG. 27. *Diplorhinotrichum candidulum*, conidiophores and conidia from Hughes (54); ×1000.

Cercospora and *Isariopsis*, however, are otherwise similar with respect to conidium origin and development and should appear together in any classification. In the hyperparasitic species assigned to *Arthrobotryum*, for want of a better generic name, the conidiophores are in synnemata and the conidia develop as in *Isariopsis*; the type species of *Arthrobotryum* is included in Section III because it has a different type of conidium development. *Phaeoisaria cornui* (Bain.) Mason is another species which produces synnemata and classified here in Section II; it produces amerospores whereas the synnematous *Sclerographium aterrimum* Berk. produces dictyospores (Hughes (60)).

In species usually with mononematous branched conidiophores, conidium production is often restricted on specialized terminal and lateral unicellular sporogenous cells and these are more or less cylindrical, subulate, or flask-shaped. In *Tritirachium* (Fig. 33) and *Calcarisporium* (Hughes (51)) the more or less subulate sporogenous cells are terminal and also in regular verticils below the uppermost septa of the main stalk and they form a wide angle with it. In the *Verticicladium* conidiophores of *Desmazierella acicola* Lib. (Fig. 28)

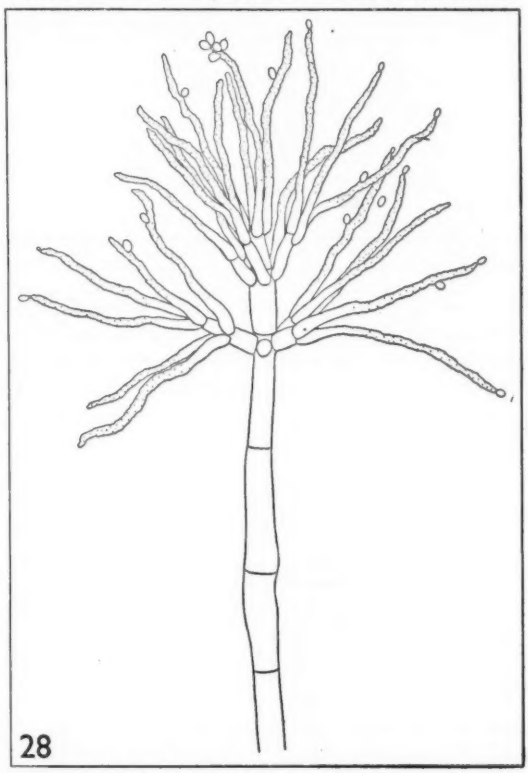


FIG. 28. *Desmazierella acicola*, conidiophore from pure culture, from Hughes (51); ×500.

the subulate sporogenous cells are borne apically and subapically on secondary lateral branches, themselves borne terminally and in whorls on primary branches.

In *Verticicladiella abietina* (Peck) Hughes (Fig. 29; see also p. 653) long subulate conidiophores bear a slimy head of conidia; primary, secondary, and tertiary branches are adpressed to the main stalk and these bear slightly divergent subulate sporogenous cells which bear conidia as in the *Verticicladium* conidiophores of *Desmazierella acicola*. The presence or absence of slime is used to differentiate the two genera.

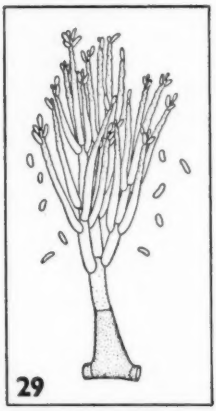


FIG. 29. *Verticicladiella abietina*, short conidiophore, and conidia from pure culture (DAOM 33941); ×1000.

Verticils of sporogenous cells are characteristic of *Costantinella* spp. (Fig. 34) (see Nannf. & Eriks. (89)) and some species of *Hansfordia* (Hughes (51)) and *Nodulisporium* e.g. conidial *Daldinia concentrica* (Bolt. ex Fr.) Ces. & de Not. as described and figured by Molliard (88). In other species of *Hansfordia* and *Nodulisporium*, and in *Virgaria nigra* Nees (Fig. 30) the

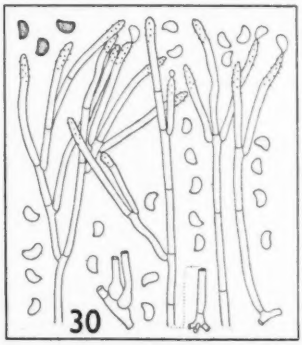


FIG. 30. *Virgaria nigra*, conidiophores and conidia (I.M.I. 40653(2)); ×500.

branching is more or less irregular and the laterals which are fertile are not particularly well differentiated. **Virgaria lignatilis** (Schw.) comb. nov.* is apparently not uncommon in Eastern North America and differs from *V. nigra* only in its shorter conidiophores and slightly smaller conidia.

In *Atractina biseptata* v. Höhnel (Fig. 31), the type species of this genus, primary and secondary branches are crowded and closely adpressed and parallel to each other and more or less parallel also with the erect almost setose mononematous conidiophore. A compact head is thus formed and the tertiary branches take the form of subulate, hyaline sporogenous cells which produce a succession of conidia in slime from a succession of new growing points; at maturity the conidia become 2-septate and the central cell brown, the outer ones remaining more or less hyaline or becoming very pale brown and collapsing readily.†

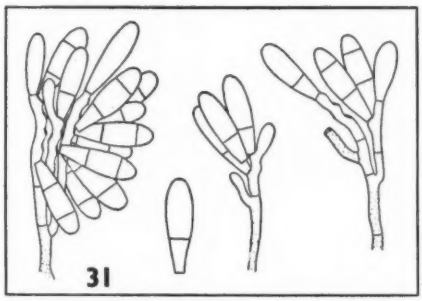


FIG. 31. *Atractina biseptata*, conidiophores and conidia from pure culture (DAOM 29146); ×1000.

Most of the Helicosporeae as treated by Linder (77) may be classified in Section II. In *Helicosporium vegetum* Nees ex Fr.§ the conidia arise in succession on short hyaline lateral sporogenous cells found towards the base of conidiophores but above, only solitary conidia may arise—on short denticles. The succession of conidia is particularly evident in *H. aureum* (Corda) Linder

* ≡ *Cladosporium lignatile Schw. in Trans. Am. Phil. Soc. II, 4 : 277. 1832.*
= *Botrytis fuliginosa Cooke & Ellis in Grevillea, 6 : 5. 1877.*
= *Botrytis atrofumosa Cooke & Ellis in Grevillea, 6 : 90. 1878.*
≡ *Virgaria atrofumosa (Cooke & Ellis) Sacc. in Sylloge Fungorum, 4 : 281. 1886.*

† *From a study of published descriptions and illustrations it seems very probable to me that Atractina biseptata will finally give way to a much earlier specific epithet and generic name. The following tentative synonymy is being considered at present in Herb. DAOM.*
? = *Graphium macrocarpum Corda in Icones Fungorum, 3 : 13. 1839.*
≡ *Haplographium macrocarpum (Corda) Sacc. in Sylloge Fungorum, 4 : 620. 1886.*
? = *Stachybotrys elata Sacc. in Michelia, 2 : 560. 1882.*
≡ *Sterigmatobotrys elata (Sacc.) Oud. in Nederl. Kruidk. Arch. II, 4 : 548. 1886.*
≡ *Phragmostachys elata (Sacc.) Cost. in Les Mucédinées simples, p. 97, Paris. 1888 [ex errore sub 'P. atra'].*
? = *Scopularia venusta Preuss in Linnaea, 24 : 133. 1851 (see Bayliss Elliott (7)).*

§ *Whilst at the Commonwealth Mycological Institute I germinated the ascospores of Ophionectria cerea (Berk. & Curt.) Ell. & Everh. and pure cultures were obtained. These cultures produced conidiophores and conidia identical with those obtained previously from the cultures prepared from conidia of what was at that time referred to Helicosporium vegetum.*

(sensu Linder) in which the sporogenous cells are swollen. In *Helicoma mülleri* Corda and other *Helicoma* spp. the conidia may arise on short lateral, finally geniculate branches or in succession on the elongating main stalk of the conidiophore; the lateral sporogenous cells are particularly conspicuous in *H. proliferens* Linder. *Helicomyces roseus* Link ex Fr. (Fig. 32) produces conidia successively at the apex of each new growing point of the conidiophore.

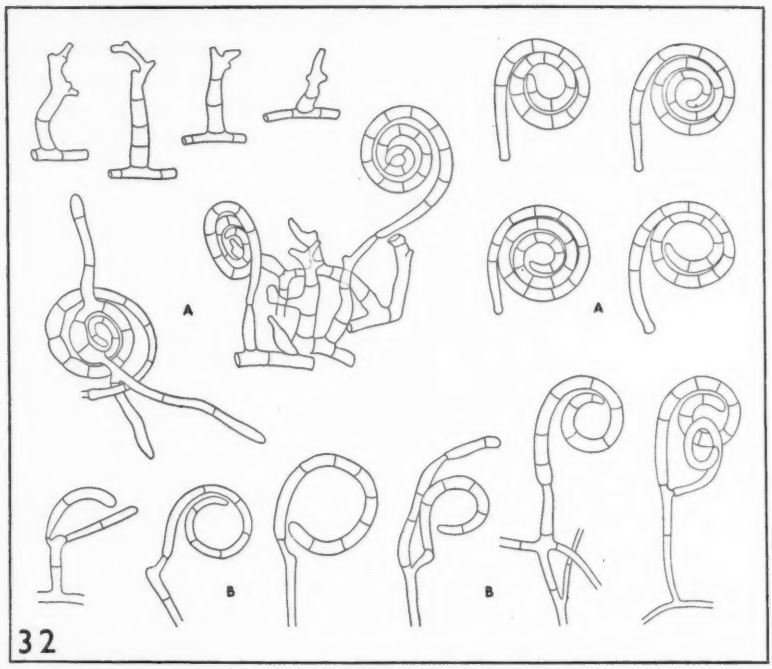
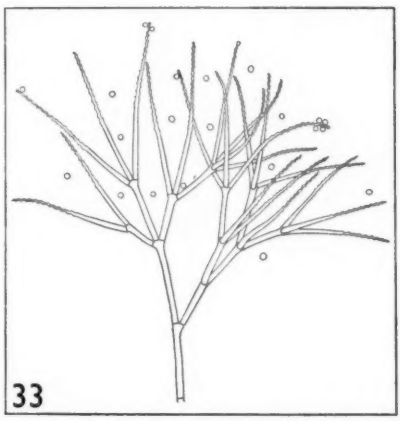


FIG. 32. *Helicomyces roseus*, mycelium, conidiophores, and conidia (I.M.I. 6054(*a*)); *A*, from the host, one conidium is germinating; *B*, from pure culture; ×500.

In most of the conidiophores and sporogenous cells that I have observed, the scars are generally distributed along the sides of the fertile region but I have not observed any spiral arrangement with any degree of certainty. In the conidiophores of *Cymadothea trifolii* the successive new growing points are produced regularly to one side so that after conidia have formed and fallen away the conidial scars are unilateral. In *Tritirachium* spp. (e.g. **Tritirachium hydnicola** (Peck) comb. nov.* (Fig. 33)) and *Beauveria* spp. the conidia are produced regularly to the left and to the right and the fertile region of the sporogenous cell resembles the rachis of a wheat ear and may be conspicuously zigzag. This is characteristic also of *Helminthosporium guareicola* Stevens

* ≡ *Virgaria hydnicola Peck in N.Y. State Museum Rept., 42 : 32. 1889.*
= *Clonostachys dichotoma A. L. Smith in Trans. Brit. Mycol. Soc. 6 : 56. 1918.*

(Fig. 22) in which two or three zigzag fertile portions may be separated by short cylindrical regions which bear no scars and the planes of the separate fertile regions may be different. In *Calcarisporium arbuscula* Preuss, on the other hand, the new growing points develop less regularly and close together in succession so that the restricted fertile region may become swollen, and after the conidia have fallen this is strongly denticulate in all directions (Hughes (51)); occasionally, however, an irregular zigzag apex may result from successive conidium production. In *Costantinella tillettei* (Desm.) Mason & Hughes and in **Costantinella micheneri** (Berk. & Curt.) comb. nov.* (Fig. 34) a single (or double?) row of conidia is produced in linear succession on a somewhat bulbous and eventually recurved apex of the sporogenous cells; such cells are so characteristic that the term *cervix* (pl. *cervices*) was proposed for them by Nannfeldt and Eriksson (89).



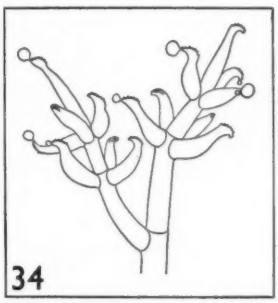


FIG. 33. *Tritirachium hydnicola*, conidiophore and conidia from the type collection; ×500.

FIG. 34. *Costantinella micheneri*, portion of conidiophore, and conidia (DAOM 29409); ×750.

In a number of species, and sometimes genera, the conidia are borne on short stalks and after the conidia have fallen these remain as denticular continuations of the conidiophores; such denticles are characteristic of *Diplorhinotrichum*, *Hansfordia*, *Calcarisporium*, *Phaeoisaria*, *Cacumisporium*, and a number of *Fusicladium* spp.

In species of *Brachysporium* (Fig. 23) and *Camposporium* (Hughes (46)) the conidia are borne on stalks which are cut off by two septa from conidiophore and conidium thus delimiting a separating-cell. In *Beltrania* the separating-cells are much swollen and well differentiated structures (Hughes (54)).

* ≡ *Botrytis micheneri Berk. & Curt. apud Berk. in Grevillea, 3 : 111. 1875.*
= *Verticillium candidum Peck in N.Y. State Museum Rept., 34 : 48. 1883 [as 1881].*
= *Costantinella athrix Nannf. & Eriks. in Svensk. Bot. Tidskr. 46 : 122. 1952.*

In **Streptothrix globosa** (Schw. ex. Fr.) comb. nov.* brown, rough-walled conidia are each borne on a very short separating-cell in succession on the main branches of the much branched conidiophores (Fig. 35) or on the very short predominantly fertile side branches.

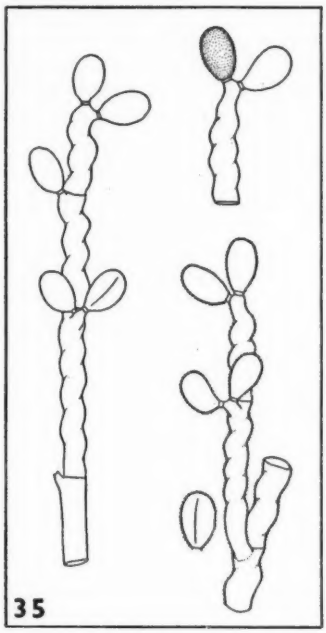


FIG. 35. *Streptothrix globosa*, portions of conidiophores, and conidia (DAOM 34510); ×1000.

* ≡ *Trichoderma globosum Schw. in Syn. Fung. Carol. Super. p. 77. 1822.*
≡ *Trichoderma globosum Schw. ex. Fr. in Systema Mycol. 3 : 215. 1829.*
≡ *Oidium inquinans Schw.* [*nom. nov.*] *in Trans. Am. Phil. Soc. II, 4 : 286. 1832.*
≡ *Torula inquinans* (*Schw.*) *Sacc. in Sylloge Fungorum, 4 : 251. 1886.*
= *Streptothrix atra Berk & Curt. apud Berk. in Grevillea, 3 : 107. 1875.*
= *Trichosporium densum Karst. in Hedwigia, 23 : 59. 1884.*
= *Strumella cornyeoidea Sacc. & Wint. in Fungi europaei no. 2984. 1883.*
= *Streptothrix pereffusa Sumstine in Mycologia, 6 : 34. 1914.*

In Herb. DAOM this species is being at present identified on Acer, Betula, Carpinus, Carya, Castanea, Cornus, Corylus, Crataegus, Fagus, Hicoria, Juglans, Quercus, and Tilia. On Quercus and Castanea, in particular, characteristic tubercularіaceous stromata are formed but on the other hosts longer conidiophores are borne on much smaller stromata; I take this to be a host reaction. Davidson (27) published strong evidence in favor of Urnula craterium (Schw.) Fr. being the ascigerous state of Streptothrix globosa (as Strumella coryneoidea). In Streptothrix globosa the conidia are nearly always coarsely roughened and they possess one or two longitudinal slits in the outer wall. In S. mounceae Sumstine the conidia do not possess a slit but a thin, paler, more or less circular area of outer wall just above the base. S. abietina Peck is closely related to but distinct from S. globosa; the wall of the conidium is conspicuously roughened and bears an apical or subapical germ pore.

Pseudocamptoum fasciculatum (Cooke & Massee) Mason* (see also p. 644) is related morphologically to *Streptorhrix* in that the conidia show similar successive development and possess a longitudinal germ slit.

In *Dicranidion fragile* Harkness (Fig. 36), the type species of *Dicranidion* Hark. (syn. *Pedilospora* v. Höhnel), hyaline staurospores are produced in succession as the blown-out ends of successively developing growing points of the conidiophores. This is the only genus known to me in which staurospores develop in this particular manner.

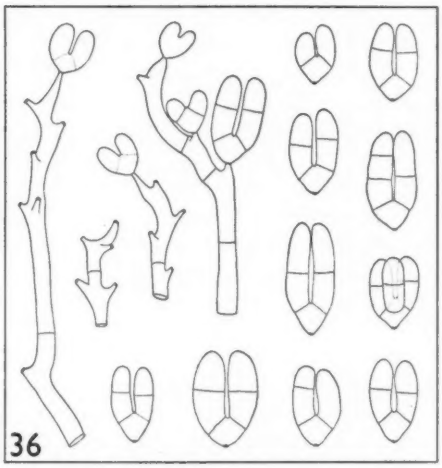


FIG. 36. *Dicranidion fragile*, conidiophores and conidia from the type collection; ×1000.

The primary conidia occasionally produce acropetal chains in Section II; thus in *Ramularia* spp., e.g. *R. onobrychidis* Allesch., each primary conidium (borne directly on the conidiophore) produces a simple or branched chain of conidia in acropetal succession. Similarly in *Heterosporium* spp., acropetal chains may develop from the primary conidia which develop in succession as the blown-out ends of successive new growing points of the conidiophore; some species of this genus have been redescribed and the development of the conidia nicely portrayed by Jacques (72). De Vries (30) transferred most of these to *Cladosporium*.

* = *Sporostachys maxima Sacc. in 'Not. Myc. xxiii in Atti Acad. ven.-trent.-istr. p. 92. 1917.'*
= *Melanographium maximum* (*Sacc.*) *Sacc. in Syloge Fungorum, 25 : 937. 1931.*

This species is based on C. F. Baker, Fungi Malayana no. 394 sub Sporostachys maxima. Sporostachys is an earlier generic name for Pseudocamptoum and so in all probability is Melanographium Sacc. based on M. spleniosporum Saccardo (101). Mason (82) suggested a still earlier name Cordella Speg., based on C. spinulosa Speg., as being a probable synonym; until the types of the original species of Cordella are examined collections in Herb. DAOM are disposed as Pseudocamptoum fasciculatum.

The conidia in this section are usually dry but they develop in slime in *Verticicladiella abietina* (Peck) Hughes (see p. 653), *Cacumisporium tenebrosum* Preuss (Fig. 37), and *Atractina biseptata* v. Höhnel whilst the conidia are by no means dry in *Helicosporium* spp.* The species included in Section II produce amerospores, didymospores, phragmospores, dictyospores, helicospores, or staurospores.

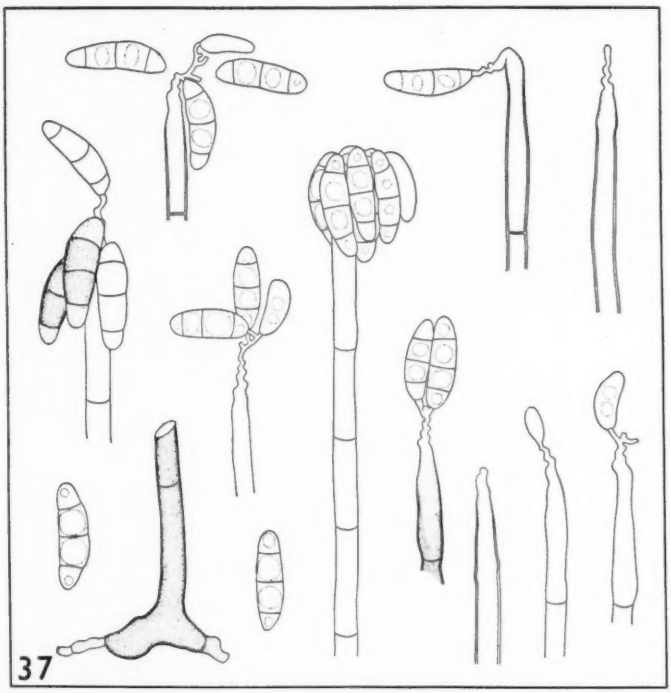


FIG. 37. *Cacumisporium tenebrosum*, conidiophores and conidia (I.M.I. 18435(*b*)); ×500.

Biggs (8) described and illustrated the successive sympodial production of conidia (as 'oidia') on conidiophores ('oidiophores') in *Corticium coronilla* v. Höhnel & Litsch.

Twyman (111) described the acervuli of *Colpoma quercina* (Fr.) Wallr. and the conidia were shown to arise in the manner characteristic of Section II but the type of conidial fructification was not identified with any separately named member of the 'Melanconiaceae'. As far as I am aware the production of conidia on immersed conidiophores by this method is not common.

* *In Herb. DAOM three species included in Helicosporium by Linder (77) are considered best classified in the apparently dry spored genus Drepanospora Berk. & Curt. e.g. D. pannosa Berk. & Curt. (= Helicosporium serpentinum Linder), and the Drepanospora conidia of Lasiosphaeria nematospora Linder and L. elinorae Linder.*

Section III

In this Section are classified fungi whose conidiophores bear a solitary apical usually thick-walled and colored conidium on the main stalk or its branches thereby terminating growth. A plurality of conidia develops from a single conidiophore or single branch only by its proliferation *through* the conidial scar left by the previous conidium with the development of a conidium on the proliferation; by a repetition of this proliferation a succession of conidia is produced accompanied by a successive increase in length of the conidiophore. This increase in length, therefore, occurs by a different method from that described for Section II. When such proliferations and conidium production occur the conidia may not be markedly thick-walled more especially when they are produced in slimy heads.

The mycelium is generally immersed, sometimes superficial.

The conidiophores show considerable variation throughout the Section and is best illustrated by reference to various species. In *Trichocladium opacum* (Corda) Hughes (62) (Fig. 38) the conidiophore may be so small as to be virtually absent as when a conidium is borne directly on one of the semi-immersed mycelial cells; alternately a conidiophore composed of up to three short cells may be developed but even so it is little different from the mycelium. *T. asperum* Harz also shows considerable variation in its conidiophores. In both species of *Trichocladium* the conidia are solitary and as in all members of Section III they develop as blown-out ends.

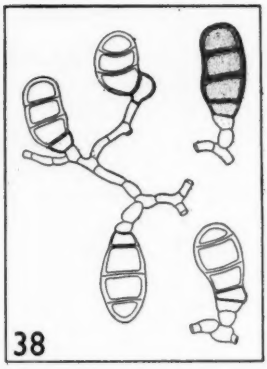
In some species of *Sporidesmium*, e.g. *S. larvatum* Cooke & Ell. (Fig. 39), the conidiophores may be constantly very short but in others, e.g. **Sporidesmium folliculatum** (Corda) Mason & Hughes comb. nov.* (Fig. 40) they may be as long as the conidia.

In *Coniosporium paradoxum* (Corda) Mason & Hughes (Hughes (47)) (Fig. 41) simple or branched and tufted conidiophores, whose component cells become balloon-like at maturity, carry a single, terminal, more or less oval dictyospore. Similar balloon-like conidiophores are also found in '*Sporidesmium*' *nitens* Schw.**

In other fungi the conidiophores may be well differentiated, erect, more or less setose, simple, thick-walled, many times septate, and much longer than the conidia; these are found in *Monosporella setosa* (Berk. & Curt.) Hughes

* ≡ *Helminthosporium folliculatum Corda in Icones Fungorum, 1 : 13. 1837.*
= *Helminthosporium brachytrichum Cooke & Ellis in Grevillea, 6 : 6. 1877.*
= *Helminthosporium macilentum Cooke in Grevillea, 6 : 74. 1877.*
= *Helminthosporium orthospermum Sacc. & Fairm. apud Sacc. in J. Mycol. 12 : 50. 1906.*
This fungus is as common around Ithaca, N.Y., and Ottawa, Ont., as it is in Britain.

** *The late S. C. Damon (26) considered this to be an earlier name for Coniosporium paradoxum which seems to be restricted to the periderm of Betula in Europe, usually in association with the conidial state of Melanomma subdispersum (Karst.) Berl. & Vogl. (= Helminthosporium longipilum Corda = H. arbusculoides Peck!). I have collected 'Sporidesmium' nitens a few times around Ottawa, Ont., and Ithaca, N.Y., on bare wood but never on the periderm of Betula although Melanomma subdispersum is exceedingly common around Ottawa on this host. The european collections of Coniosporium paradoxum are sufficiently distinct from 'Sporidesmium' nitens to merit their being kept separate until pure cultures prove them to be the same.*



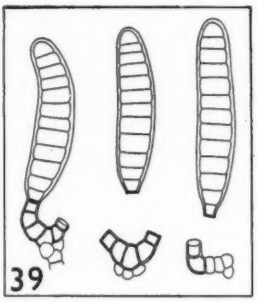
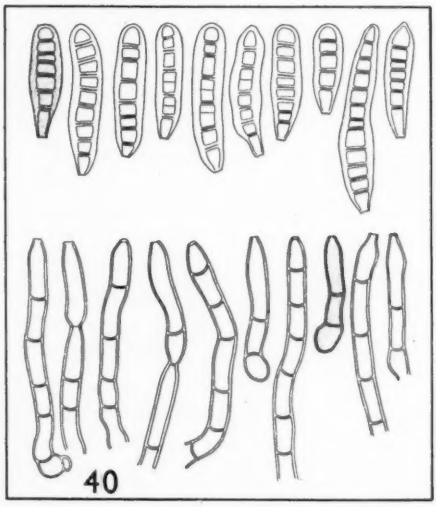


FIG. 38. *Trichocladium opacum*, mycelium, conidiophores, and conidia from Hughes (62); ×500.

FIG. 39. *Sporidesmium larvatum*, conidiophores and conidia (Ellis, N. Am. Fungi, no. 355, on cedar rails); ×500.



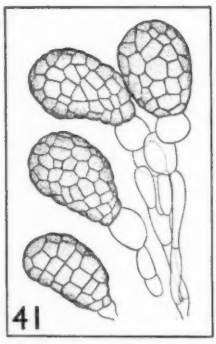
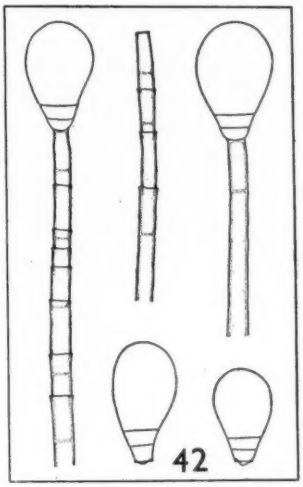


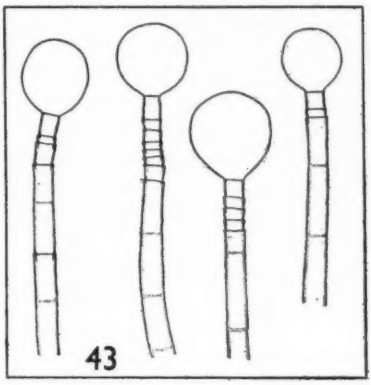
FIG. 40. *Sporidesmium folliculatum*, conidiophores and conidia (I.M.I. 5505); ×500.

FIG. 41. *Coniosporium paradoxum*, conidiophores and conidia from Hughes (47); ×500.

(Fig. 42, and see also p. 654), in *M. sphaerocephala* (Berk. & Br.) Hughes (Fig. 43, and see also p. 654), and in *Farlowiella carmichaeliana* (Berk.) Sacc. (Fig. 44).

In *Bactridium flavum* Kunze (Fig. 45) and *B. fulvellum* Berk. the conidiophores are tufted and form a tuberculariaceous fructification; each conidiophore is more or less irregularly branched and is in fact a more or less undiffer-





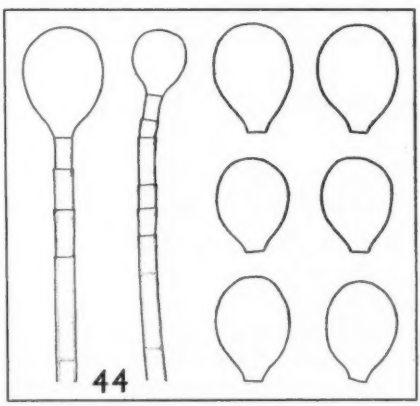
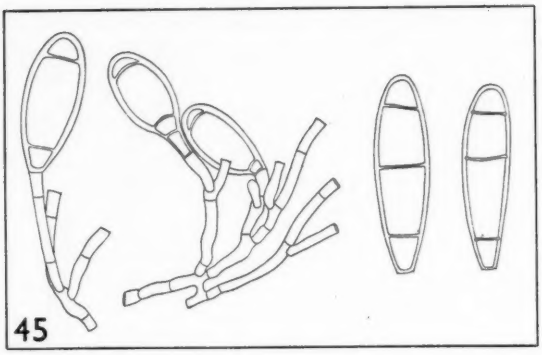


FIG. 42. *Monosporella setosa*, conidiophores and conidia (DAOM 29291(*a*)); ×500.
FIG. 43. *Monosporella sphaerocephala*, conidiophores and conidia (DAOM 29423(*a*)); ×500.
FIG. 44. *Farlowiella carmichaeliana*, conidiophores and conidia (I.M.I. 7040); ×500.

entiated, septate, aerial, branched hypha bearing solitary apical conidia. In Section III, I classify *Allescheriella crocea* (Mont.) Hughes (50) (Fig. 46) which seems to be morphologically related to *Coccospora agricola* Goddard (White and Downing (115)). *Allescheriella crocea* has wide mycelium and its affinities may well be with the Basidiomycetes. Linder (78) included this fungus as '*Oidium simile* Berk.' (see Hughes (50)) but the development of thick-walled conidia on lateral branches, not denticles, places the fungus in Section III.



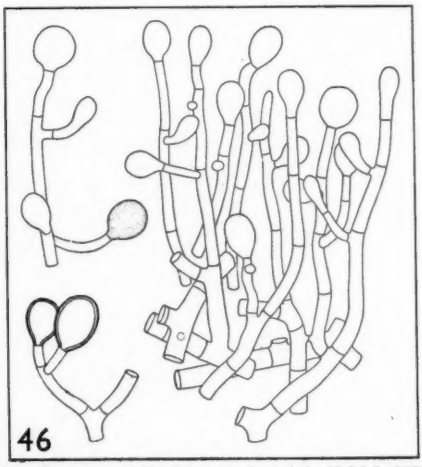


FIG. 45. *Bactridium flavum*, conidiophores and conidia (I.M.I. 33713); ×200.
FIG. 46. *Allescheriella crocea*, conidiophores and conidia from Hughes (50); ×500.

In *Arthrobotryum stilboideum* Cesati (Hughes (55)) and *Leptographium lundbergii* Lagerb. & Melin a more or less penicillate type of branching is observed; the conidiophores are synnematous and simply penicillate in the first and mononematous and repeatedly penicillate in the second; slimy heads of conidia are produced by both. *Stysanus* produces synnematous fructifications and the branching is subpenicillate being most evident at the ends of the central conidiophores. *Scopulariopsis* differs from *Stysanus* mainly in the absence of synnemata but dry conidia develop in both.

The genus *Phragmocephala* Mason and Hughes (85) is included in this Section; the species have mononematous, synnematous, or more or less tuberculariaceous conidiophores. It appeared to the authors of this name that the three generic names required for such species in the Saccardoan scheme would separate obviously related species.

Now the important feature of Section III is the development first of a solitary conidium at the apex of the conidiophore and its branches thus terminating their growth. There can usually be observed direct continuity between the wall of the conidiophore and that of the conidium. In most cases only a single conidium is produced at each end as in *Phragmocephala* (excluding *P. setosa*, see p. 654), *Bactridium* spp., and some *Sporidesmium* spp. Whereas acropetal chains of conidia are found in Sections I, II, and VI (p. 629) I have never found them in this present Section. A plurality of conidia in Section III can arise only as explained below.

In the West African *Annellophora africana* (Hughes (57)) (Fig. 47), for

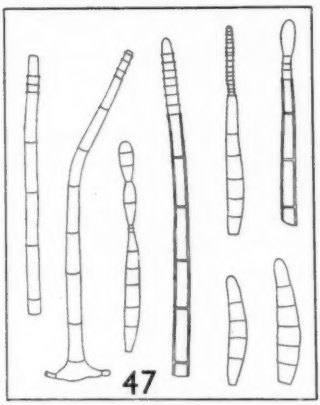


FIG. 47. *Annellophora africana*, conidiophores and conidia from Hughes (57); ×500.

example, the first conidium is terminal and after seceding the conidiophore proliferates *through* the terminal scar and the apex of the proliferation blows out into another conidium which is cut off from the proliferated conidiophore by a septum; this septum appears at a variable distance above the scar of the first conidium. A series of such proliferations with a single conidium produced at each new level results in a closely or distinctly annellated appearance of the conidiophore. Such a conidiophore with annellations is so characteristic that it is considered worth while proposing the term '*annellophore*' for it. Annellophores, indicating this curious succession of proliferations and terminal conidia are far more general in the Hyphomycetes (and perhaps the Coelomycetes) than has previously been suspected and on the whole little or no attention has been given to annellations in published descriptions and illustrations.

Annellophores which are simple, well differentiated, and septate are found in *Ceratosporella* (Hughes (53, 65)), *Triposporium* (Hughes (53)), *Monosporella* (Figs. 42, 43, 44), *Podoconis* spp. (Hughes (67, 68)), and some *Sporidesmium* spp. Arnaud (1) described his genus *Bainieria* for the single species *B. hyalina* Arn. in which he drew attention to the origin of the conidia being the same as that found in conidial *Venturia inaequalis* (Cooke) Wint. [*Spilocaea*] and *Chaetotrichum* Sydow (≡ *Annellophora* Hughes).

But annellations are by no means restricted to such unbranched and more or less setose conidiophores; they are to be found, perhaps more commonly, in other genera in which the actual sporogenous cells are unicellular and well differentiated from that part of the conidiophore that supports them, or a distinct support for them may be absent especially in some foliicolous species.

In conidial states referable to *Spilocaea*, *Mastigosporium*, *Stigmina*, *Pollaccia*, and *Deightoniella* (Hughes (59, 69)), all leaf parasites, the annellophores are usually short, single-celled, more or less cylindrical or flask-shaped structures. In *Spilocaea* states the annellations are very conspicuous, but the reverse is true of *Pollaccia* and *Mastigosporium* in which the annellophores are hyaline or subhyaline. In leaf parasites such as these there is an advantage in producing short conidiophores in view of their exposed position. I have also seen conspicuous annellations in the *Septoidium* conidiophores of some species of *Parodiopsis*.* These form-genera are scattered throughout the Saccardoan classification.

On the other hand annellations are characteristic of the sporogenous cells which are supported on distinct mononematous or synnematous stalks. In *Scopulariopsis brevicaulis* (Sacc.) Bain. (Fig. 48, *A-D*), which may be regarded as the type species of this genus, the sporogenous cells are annellophores; they have been called phialides and also 'sterigmata' (as in *Penicillium*) but neither term seems to me to be suitable. When young, the annellophores are flask-

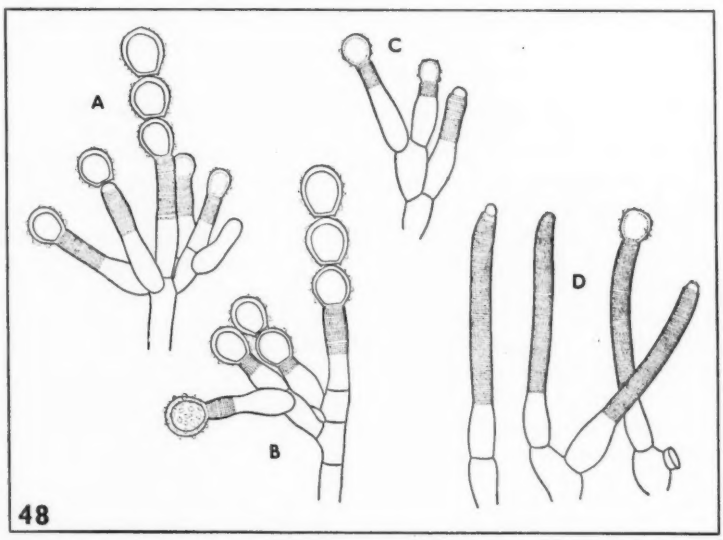


FIG. 48. *Scopulariopsis brevicaulis*, conidiophores and conidia; DAOM 29102, *A*, *B*, from pure culture four weeks old: DAOM 33997, *C*, from two-weeks-old pure culture; *D*, from eight-weeks-old culture; ×1000.

* *In addition to the Septoidium conidia, most Parodiopsis spp. produce microconidia on long conidiophores by the method characteristic of Section II.*

shaped with a short, almost cylindrical neck (Fig. 48, *A*, *B*, *C*); in older annellophores (Fig. 48, *D*) the necks are longer by virtue of the greater number of annellations. The conidia have a flattened base encircled by a minute frill; they persist in long fragile chains but these are not true chains in the sense that those of *Xylohypha nigrescens* (Fig. 1) or *Septonema secedens* (Fig. 4) are true chains. It is interesting to note that most illustrations of *Scopulariopsis* spp. show the cylindrical ends of sporogenous cells and the descriptions usually give a wide range for the length of sporogenous cells; this is to be expected considering the method of conidium production. Characteristic of false basipetal chains is the fact that the conidium at the apex of the annellophore is more or less mature before the new one developing below detaches it from the annellophore. The occurrence of chains of conidia developing from annellophores is facultative but obligate in *Xylohypha*, *Bispora*, and indeed all other fungi producing acropetal chains.

The sporogenous cells of *Stysanus** *stemonitis* (Pers. ex Fr.) Corda (Fig. 49) have been called phialides but close examination will show them to be annellophores, with the annellations by no means inconspicuous. As with *Scopulariopsis* (Fig. 48) young annellophores have very short cylindrical necks which increase in length as successive annellations develop. Similar annellations are found in **Stysanus purpureofuscus** (Fr.) comb. nov.** (Fig. 50) and *Trichurus gorgonifer* Bain. (Fig. 51).

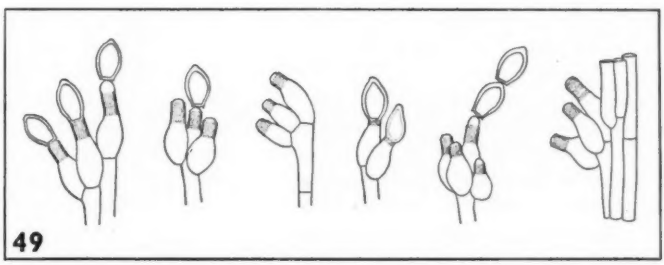


FIG. 49. *Stysanus stemonitis*, portions of synnema, and conidia (I.M.I. 22419): ×1000.

Phaeoscopulariopsis Ota (95) was published for two species, *P. paisii* (Poll.) Ota (≡ *Torula paisii* Poll.) and *P. bestae* (Poll.) Ota (≡ *Torula bestae* Poll.). I have seen an isolation of *Phaeoscopulariopsis paisii* (I.M.I. 36480) and the sporogenous cells are annellophores. Now this genus is precisely

* *In Pycnostysanus azaleae (Peck) Mason the dry head of conidia is on a stalk as in Stysanus but the conidia develop in acropetal chains as in Xylohypha (Section IA, p. 582) and not from annellophores. Pycnostysanus must be classified in Section IA.*

** ≡ *Aspergillus purpureofuscus Fr. in Systema Mycologicum, 3 : 388. 1832.*
≡ *Aspergillus purpureofuscus Schw. in Trans. Am. Phil. Soc. II, 4 : 282. 1832.*

There seems to be no doubt that Fries obtained a specimen from Schweinitz and I consider both names to be based on the same collection, being thereby obligate synonyms. I.M.I. 34001(c) (Fig. 50) is the same thing.

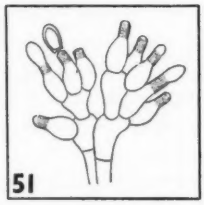


FIG. 50. *Stysanus purpureofuscus*, portion of synnema (I.M.I. 34001(*c*)); ×1000.
FIG. 51. *Trichurus gorgonifer*, portion of synnema, and conidia (I.M.I. 7393); ×1000.

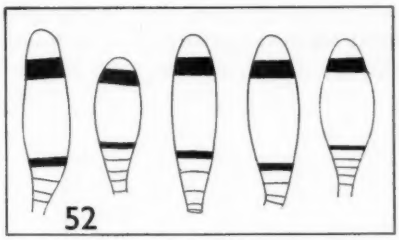
Scopulariopsis with dark colored conidia and is an earlier name for *Masoniella* G. Smith (107) which is based on *M. grisea* (Smith) Smith. The type isolation of *M. grisea* (DAOM 29438) produces chains of conidia from annellophores.

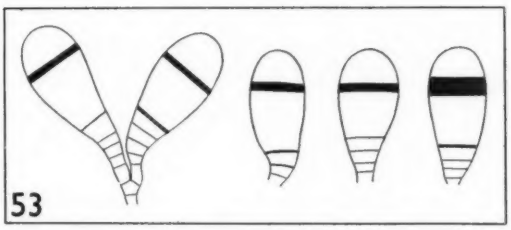
It was suggested by Hughes (55) that the sporogenous cells of *Arthrobotryum stilboideum* Cesati bore annellations; of this I am now convinced following an examination of an isolation of this fungus. In pure culture *A. stilboideum* produces a black slimy mass of conidia; the synnemata are not well differentiated but the annellations on the end cells of the conidiophores can be observed more readily.

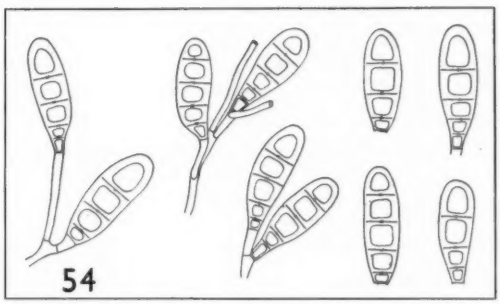
The genus *Bactrodesmium* is of particular interest as a member of Section III; it seems to be separable from *Bactridium*, type species *B. flavum* (Fig. 45), only on account of its dematiaceous conidia. In *B. flavum*, *Bactrodesmium abruptum* (Berk. & Br.) Mason & Hughes (Fig. 52), *B. fasciculare* (Corda) Mason & Hughes (Fig. 53), and **Bactrodesmium spilomeum** (Berk. & Br.) Mason & Hughes comb. nov.* (Fig. 54) the conidia are solitary on the ends of branched conidiophores; in *B. masonii* Hughes (Fig. 55, and see also p. 654), however, the conidiophores are likewise branched but grow through the conidial scars of former conidia to produce a proliferation whose apex swells out into another conidium. Two or three conidia may be formed in this way on what may now be called annellophores in this species. When an apparent chain of two conidia is observed (Fig. 55), and this is not uncommon, then this is a false chain, homologous with that produced by *Stysanus stemonitis* or *Scopulariopsis brevicaulis*, the conidia having developed in basipetal succession. The production of annellations in *Bactrodesmium masonii* and their absence in the closely related *B. spilomeum* is further evidence to support the inclusion, in one Section, of those fungi which produce solitary conidia and those which produce a succession from annellophores. Conidiophores with and without annellations are also found in the different species of *Podoconis* (Hughes (67, 68)) and *Sporidesmium*; for example, they are absent in *Podoconis macrura* (Sacc.) Hughes and *Sporidesmium folliculatum* (Fig. 40) but are

* ≡ *Sporidesmium spilomeum Berk. & Br. apud Rabenhorst in Fungi europaei, no. 1162. 1868.*

This name was omitted from Saccardo's Sylloge Fungorum and from the List of British Hyphomycetes (Wakefield and Bisby (112)), but it was one of the two species mentioned when Cooke proposed the new name in Grevillea, 12 : 35. 1883, the first being S. abruptum Berk. & Br.







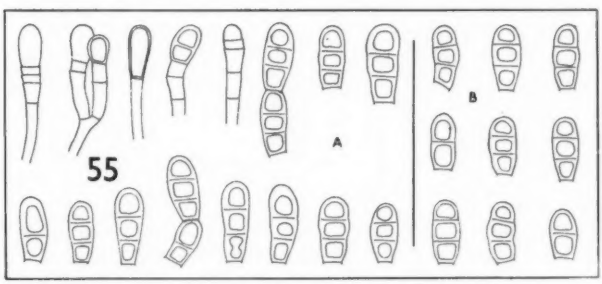


FIG. 52. *Bactrodesmium abruptum*, conidia (I.M.I. 19039); ×500.

FIG. 53. *Bactrodesmium fasciculare*, conidia (I.M.I. 14014); ×500.

FIG. 54. *Bactrodesmium spilomeum*, conidiophores and conidia (I.M.I. 14486); ×500.

FIG. 55. *Bactrodesmium masonii*, conidiophores and conidia; *A*, from I.M.I. 19219(*y*); *B*, I.M.I. 19652(*c*); ×500.

produced in *Podoconis bicolor* Hughes, *P. alta* (Preuss) Mason & Hughes (Fig. 56), and in **Sporidesmium densum** (Sacc. & Roum.) Mason & Hughes comb. nov.* (Fig. 57).

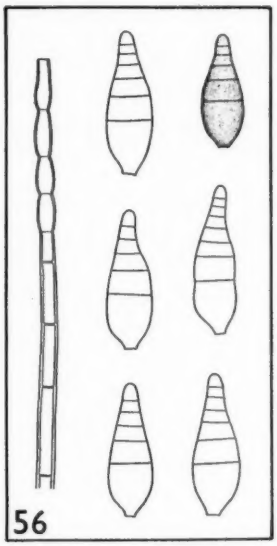


FIG. 56. *Podoconis alta*, conidiophores and conidia from Hughes (67); ×500.

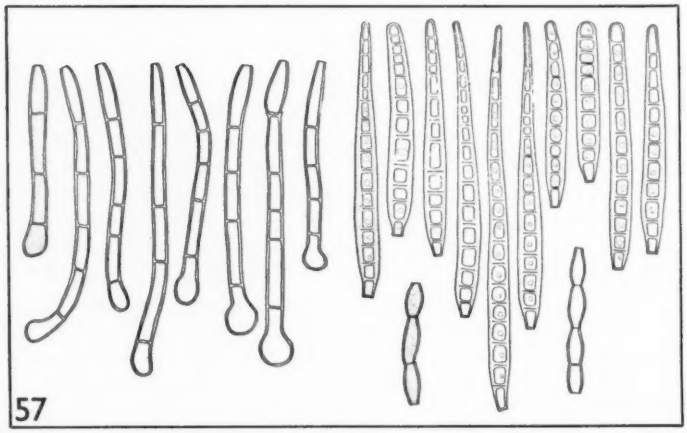


FIG. 57. *Sporidesmium densum*, conidiophores, detached annellations, and conidia (I.M.I. 6784); ×500.

* = *Helminthosporium densum Sacc. & Roum. in Rev. Mycol. 3 : 29. 1881.*

In **Thyrostromella negundinis** (Berk. & Curt.) comb. nov.* the subhyaline annellophores form a compact palisade on an erumpent stroma; the conidia are 2-septate and brown. **Thyrostromella pedunculata** (Ell. & Everh.) comb. nov.** (Fig. 58) is only critically distinct from *T. negundinis* on their

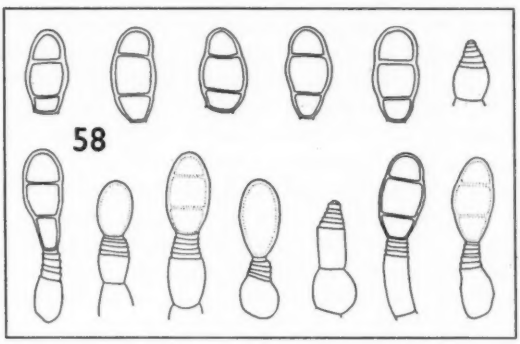


FIG. 58. *Thyrostromella pedunculata*, conidiophores and conidia (DAOM 1749); ×500.

respective hosts, *Sambucus* and *Acer negundo*, although pure cultures may show them to be identical. In *T. pedunculata* the annellophores are brown and annellations very conspicuous with their diameter decreasing perceptibly with each successive conidium. The conidia are dry, 2-septate, slightly constricted, thick- and dark-walled, rounded at the apex, and flattened at the base which bears a conspicuous frill. In **Thyrostromella sambucina** (Ell. & Everh.) comb. nov.† (Fig. 59) the annellations on the more or less cylindrical

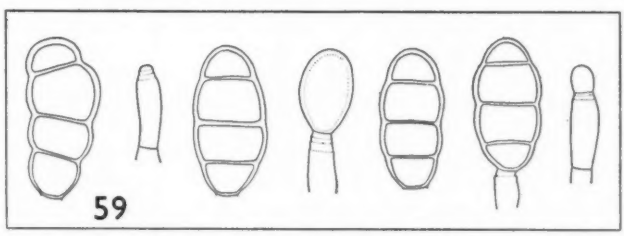


FIG. 59. *Thyrostromella sambucina*, conidiophores and conidia from the type collection; ×500.

* ≡ *Coryneum negundinis Berk. & Curt. apud Berk. in Grevillea, 2 : 153. 1874.*
= *Coryneum negundinis Ell. & Everh. in Bull. Torrey Botan. Club, 24 : 292. 1897.*
≡ *Coryneum septosporioides Sacc. & Syd. [nom. nov.] in Saccardo's Sylloge Fungorum, 14 : 1022. 1899.*

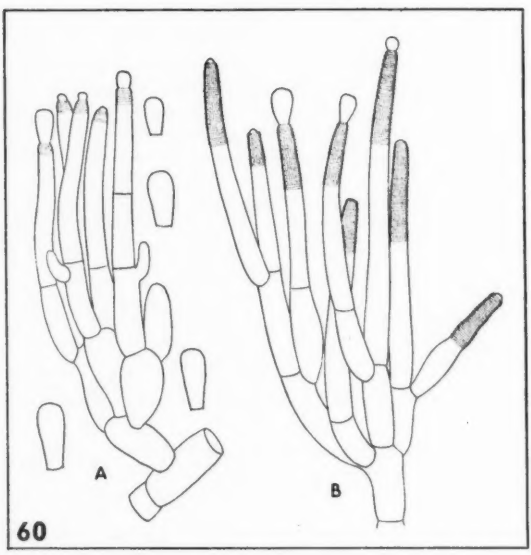
** ≡ *Brachysporium pedunculatum Ell. & Everh. in Proc. Acad. Nat. Sci. Phil. 47 : 440. 1895.*
≡ *Exosporium pedunculatum (Ell. & Everh.) W. B. Cooke in Mycologia, 41 : 617. 1950.*

† ≡ *Coryneum sambucinum Ell. & Everh. in Bull. Torrey Botan. Club, 24 : 467. 1897.*
= *Exosporium sambuci Tracy & Earle apud Greene in Plantae Bakerianae, 1 : 36. 1901.*

annellophores are not so conspicuous as in *T. pedunculata*. The conidia are 3-septate, thick- and dark-walled, slightly constricted, and somewhat flattened at the basal scar provided with a marginal frill.

In the conidia produced from annellophores it will at once be noticed (e.g. Figs. 55, 58, 59) that the majority of them have a somewhat flattened base as wide as the apex of the annellophore, with a minute frill of ruptured outer wall around it. This frill is obvious in colored conidia and is indicative of the double nature of the wall of the conidium, but the presence of the frill in hyaline conidia can more easily be observed using phase contrast equipment. The successive annellations may have a more or less constant diameter as in *Venturia inaequalis* and *Stysanus stemonitis* (Fig. 49) but in others e.g. *Thyrostromella pedunculata* (Fig. 58) successive annellations are narrower so that the width of the scars on the conidia varies accordingly.

When conidia with a flattened base and a minute basal frill are observed then close examination may show that they have developed from annellophores. Now *Leptographium lundbergii* Lagerb. & Melin (Fig. 60) for some time proved to be difficult to dispose suitably in a system of classification because conidium development was not understood; the bases of the hyaline oval-oblong conidia are somewhat flattened and bear a marginal frill around the scar. The more or less subulate or flask-shaped end cells of the mononematous penicillately branched conidiophores show the presence of extremely



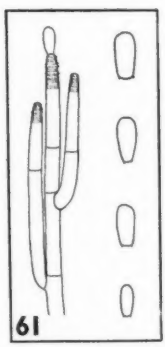


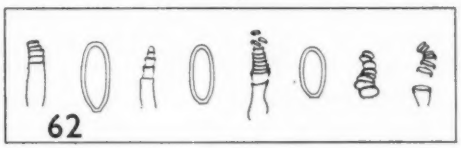
FIG. 60. *Leptographium lundbergii*, fructifications from pure culture (DAOM 22593); *A*, seven days old; *B*, 23 days old; ×1000.

FIG. 61. *Leptographium* sp., small fructification from pure culture (DAOM 28732(*b*)); ×1000.

inconspicuous annellations so they are annellophores.* The difference in length between annellophores from a seven-days-old and a 23-days-old pure culture is shown in Fig. 60. The disposition of *L. lundbergii* along with *Stysanus*, *Trichurus*, *Scopulariopsis*, and *Arthrobotryum* then became necessary and its location there seems now so very obvious and natural.

DAOM 28732 (b), an isolation from rotting timber, produces slimy heads of conidia on a mononematous conidiophore branched penicillately at the apex; in this fungus the annellations are conspicuous (Fig. 61).

Shaw and Hubert (103) regarded *Hantzschia* Auersw. to be an earlier synonym of *Leptographium*** but in this paper the former is included in Section IV because the sporogenous cells are considered to be phialides and the latter is included here in Section III because of its annellophores.



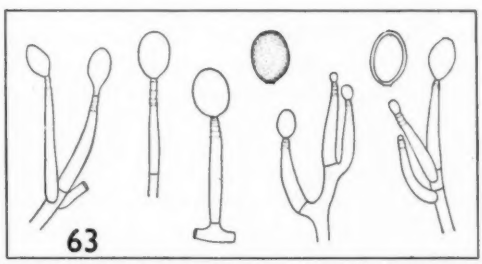


FIG. 62. *Melanconis juglandis*, conidiophores and conidia (DAOM 35198); ×500.
FIG. 63. *Melanconis stilbostoma*, conidiophores and conidia from pure culture (DAOM 28797); ×500.

In the *Melanconium* state of *Melanconis juglandis* (Ell. & Everh.) Graves (Fig. 62), and in *M. stilbostoma* (Fr.) Tul. (Fig. 63) as isolated from *Betula papyrifera* twigs in Canada I find the sporogenous cells to bear well developed annellations. This is particularly evident in *Melanconis juglandis* in which the annellations are pale brown but so delicately attached to each other that in a crushed preparation they may become detached and appear as distinct rings as shown in Fig. 62.

In a number of illustrations of cross sections of coelomycetous fructifications the sporogenous cells have been figured as more or less cylindrical with a flattened apex; furthermore, the conidia of such fungi are often shown with a flattened base and a minute marginal frill. It is not improbable that such

* *Perhaps these are the structures which Falck (35) termed 'ampliphialides'.*

** *However, these authors proposed retaining the use of Leptographium because Hantzschia Grunow had been proposed independently for a genus of diatoms; Hantzschia Grunow is a later homonyn of Hantzschia Auersw., as these recent authors pointed out, and to reverse the general procedure in view of the priority of the fungus genus would lead to confusion and has no justification whatsoever.*

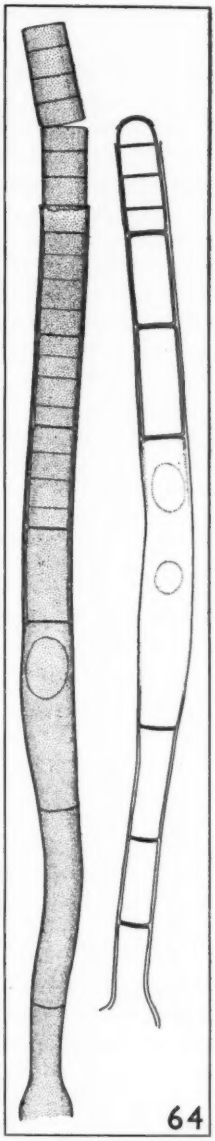
conidia will be found to have developed from annellophores. On the whole the precise method of conidium development in the Coelomycetes has been neglected, granted the conidiophores are usually extremely small, but from a few personal observations and reference to some published descriptions and illustrations I gather that they may well show the same types of development as encountered in those Fungi Imperfecti with exposed conidiophores. When the types of development in the Coelomycetes become known, the 'Melanconiales' are particularly suited for investigation, then the group may be incorporated with the Hyphomycetes and major groupings differentiated on the type of conidium development rather than on the enclosed or exposed position of the conidiophores. Mason (83) stressed the overemphasis of sporodochia, pycnidia, and acervuli in the current classification too, but my approach to this conclusion differs from his.

Section IV

In this section are included those form-species whose conidia (phialospores) develop from phialides. The term phialide is here restricted to those unicellular structures which are usually terminal, but sometimes intercalary as well, on simple or branched conidiophores; they are oval to subcylindrical to flask-shaped or subulate often with a well differentiated basal swelling and a narrower distal neck, with or without a terminal collarette; from the apex of each phialide develops a basipetal succession of phialospores without an increase in the length of the phialide itself. If the phialide does proliferate e.g. in *Catenularia* (see below), then a plurality of conidia develops at each level. Not uncommonly a phialide may possess two or three collarettes in which case the term polyphialide can be applied to it (e.g. *Lasiosphaeria hirsuta*, in Hughes (52)).

In *Sporoschisma* spp. (Hughes (45)) are found the largest phialides I have ever seen and because of their great dimensions they show clearly the events occurring during phialospore development. The stalked phialides in *S. mirabile* Berk., the type species (Fig. 64), are up to 320μ long, consist of a bulbous base leading above to a 1- to 3-septate stalk which then enlarges into a slightly swollen part which then narrows again into a more or less cylindrical tube closed at the rounded apex. Up to three phialospores are laid down within the cylindrical tube from the apex backwards; finally the thinner-walled apical cap of the phialide is torn off presumably by pressure from within. The uppermost phialospore has a rounded apex and is usually shorter and has fewer septa than the others and when pushed out from below is usually found with the torn-off apex of the phialide capping its distal end. A similar type of development can be observed also in *S. saccardoi* Mason & Hughes, *S. juvenile* Boud., and in **Chalara insigne** (Sacc., Rouss., & Bomm.) comb. nov. (≡ *Sporoschisma insigne* Sacc., Rouss., & Bomm.*).

* *Chalara insigne lacks the capitate hyphae which are so characteristic of the three species of Sporoschisma redescribed by Hughes (45); in this paper Chalara insigne was redescribed as Sporoschisma insigne. I collected this in September, 1952, in excellent condition on an old Poria in N.Y. State, U.S.*



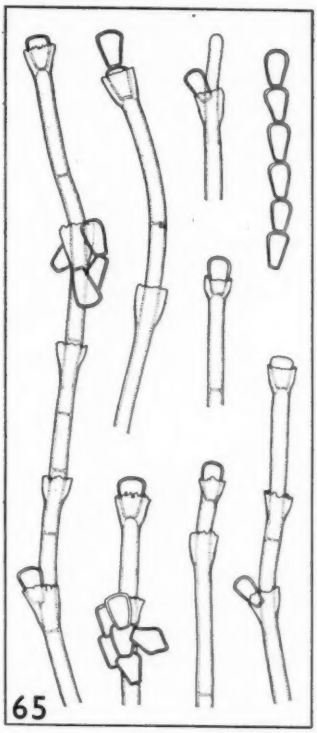


FIG. 64. *Sporoschisma mirabile*, young and mature phialides with phialospores from Hughes (45); ×500.

FIG. 65. *Catenularia cuneiformis*, phialides and phialospores (I.M.I. 49478); ×500.

Brierley (15) described the development of the 'endoconidia' of '*Thielavia basicola* Zopf' [*Thielaviopsis basicola* (Berk. & Br.) Ferr.] and the sequence of events is similar to that found in *Sporoschisma*.

In *Catenularia cuneiformis* (Richon) Mason (Fig. 65) the conidiophores are simple, erect, and at maturity bear a terminal funnel-shaped collarette and usually up to four intercalary collarettes through which the conidiophore has proliferated. The first collarette is formed by the laying down inside the slightly enlarged apex of the conidiophore of a single cuneate phialospore and the irregular breakup of the wall of the apex of the original swelling to form the funnel-shaped structure. A succession of phialospores develops as in *Sporoschisma* by the proliferation of the phialide into the collarette and the cutting off of single cell units. Phialospores generally mature before another is produced below them but this is not always so in *S. juvenile* in which the phialospores may emerge from the collarette whilst still hyaline and continuous although more distal conidia in the chain are brown and 3-septate.

In DAOM 33739 (Fig. 66), disposed for the time being with two other isolates from rots of wood of *Betula lutea* from New Brunswick (33740, 33761) as *Phialophora* sp. 4, a most interesting type of phialide fructification is found. These phialides are in penicillate fascicles; their basal part is more or less oval and at maturity each has a long, cylindrical, and conspicuous collarette.

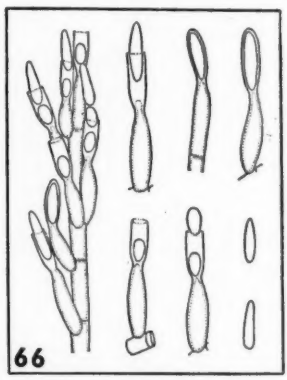


FIG. 66. *Phialophora* sp. 4, phialides and phialospores (DAOM 33739); ×1000.

Early stages show that the first phialospore which is laid down within the unbroken extension of the phialide is long and cylindric-oval; a break occurs towards the apex of the outer wall very probably because of continued growth of the first phialospore and the inability of the outer wall to grow any further. The first long phialospore is thus freed and when it has seceded the collarette becomes very evident. Subsequent phialospores are oval and only about half as long as the first phialospore or the collarette. This accounts for the two types of phialospores, the long and the short, found in all preparations of the three isolates of *Phialophora* sp. 4.

In other species of *Phialophora*, e.g. *P. fastigiata* Lagerb. & Melin (Fig. 67), the phialide may have a shorter collarette, often about a half as long as the phialospore. In most species of *Phialophora* that I have examined the first formed phialospore differs but little from the subsequent ones.

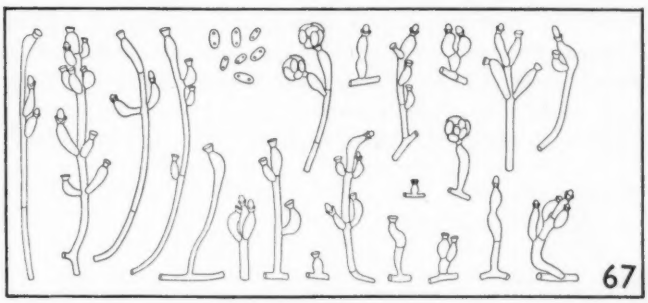


FIG. 67. *Phialophora fastigiata*, hyphae, phialides, and phialospores from Hughes (52); ×500.

It would seem, therefore, that in many phialides the first phialospore is truly endogenous and develops within the unbroken outer wall of that part of the phialide distal to the neck. After the rupture of the wall the first phialospore which, in some cases, has reached maturity, is liberated and the collarette becomes evident. The position of the break in the outer wall, originally enclosing the first phialospore will determine the length of the collarette. Subsequent phialospores are not precisely endogenous even though they may be sunken to a greater or lesser degree within the open collarette.

In *Fusarium semitectum* Berk. & Rav. (DAOM 34095, det. W. L. Gordon) the first phialospore develops as a blown-out end of the apex of a cell which is the phialide initial. No double wall can be differentiated but when this first phialospore secedes a break in the wall occurs where the initial is separated from the phialide by a constriction and a minute cylindrical collarette becomes differentiated; a barely visible frill is sometimes seen just above the base of this first phialospore and is that part of the wall which was connected to the collarette. The first formed phialospores are usually smaller and less curved than those which follow.

In *Fusariella* spp. (Hughes (44)) the phialospores remain attached in chains and each phialospore is attached to the second cell from the apex of the phialospore below it; this is due to the lateral and curved growth of that spore during development. In *F. atrovirens* Sacc. and *F. obstipa* (Pollack) Hughes it was possible to see that the apical or first formed phialospore in the chain is always straight, the subsequent ones being distinctly curved. *F. atrovirens* is illustrated in Fig. 68.

In the phialides of *Menispora* spp. the outer wall enclosing the first phialospore initial is ruptured at a very early stage when the initial is quite small so

that a distinct collarette is present during the later stages in the development of the first phialospore. In *Menispora tortuosa* Corda (Fig. 69)* and *M. ciliata* Corda, two common fungi of wood and bark in Britain, phialides are borne singly or in small groups on short stalks towards the bases of erect conidiophores which may be coiled or flexuous above. The phialides are more or less cylindric-oval and recurved at the narrowed apex so that the collarette is directed towards the base. The phialospores are 3-septate in *M. tortuosa* (≡ *Eriomenella tortuosa* (Corda) Peyronel), and continuous in *Menispora ciliata* Corda, being once ciliate at both ends in the two species; they form slimy fascicles lying alongside the phialide from which they developed.

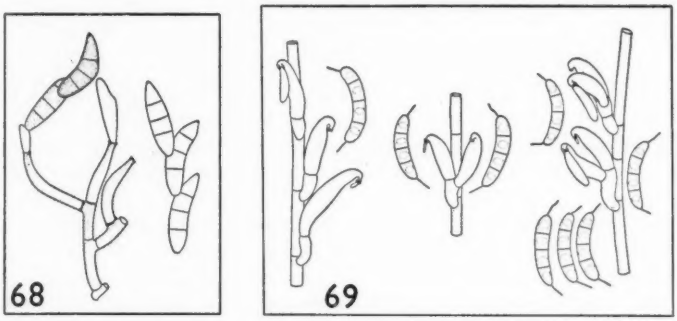


FIG. 68. *Fusariella atrovirens*, phialides and phialospores from Hughes (44); ×500.
FIG. 69. *Menispora tortuosa*, phialides and phialospores (I.M.I. 20037(*d*)); ×500.

In the *Tubercularia* fructifications of *Nectria cinnabarina* (Tode ex Fr.) Fr. the conidia-bearing hyphae are the ultimate ends of more or less verticillately branched hyphae arising from the stroma. The fertile hyphae are long, usually simple, hyaline, and septate. At the apex of these and just below most of the transverse septa are upwardly directed short branches bearing what I take to be a cylindrical collarette. The phialospores are produced successively in large numbers and result in the conspicuous orange-colored fructifications. The presence of a linear series of sporogenous cells is not common in the Hyphomycetes.

Phialide-bearing fungi are extremely numerous and no attempt can be made in a short paper to give an account of the various forms displayed by the fructifications. Some phialide-bearing species have been described by Cain (19) and Hughes (52, 58) to mention but two of numerous authors who have dealt with like forms.

* *Six recent collections in Canada (Ontario) are very close to M. tortuosa but the 3-septate phialospores are more strongly ciliate; the phialides are more numerous on the short lateral stalks, often appearing digitate, and the apex of each is not recurved so that the phialospores come to be grouped in slimy fascicles perched on the apex of the phialides and not alongside them as in M. tortuosa.*

Section V

In this section are classified those fungi which develop basipetal chains of conidia from poorly differentiated conidiophores which possess a generative or meristematic region towards the apex with the result that the conidiophore merges imperceptibly with the chain of conidium initials which exhibit a gradual maturation towards the distal end of the chain.

In 1952 Hughes (64) discussed two species, the conidial state of *Hysterium insidens* Schw. (Fig. 70) (= *Sirodesmium granulosum* de Not) and *Sirodesmium diversum* (Cooke) Hughes (≡ *Torula diversa* Cooke) (Fig. 71); these were illustrated and described. In these two species the conidial fructifications are pustular and the dry chains of dark brown conidia arise in basipetal succession from simple or branched radiating conidiophores. Close examination shows that the conidia merge imperceptibly with the conidiophores and it is impossible definitely to indicate where the conidiophore ends and conidium initials begin. This is because the conidiophore is meristematic at its upper end so that a basipetal chain of conidium initials develops; the maturation of conidia is a slow process and in *Hysterium insidens* in particular all stages from amerospores through phragmospores to large dictyospores can be seen in a single chain.

In the publication cited attention was drawn to the similarity between this type of development and that described by Yarwood (117) for the *Acrosporium* (*Oidium* auct.) conidia of the powdery mildew *Erysiphe polygoni* DC. (Fig. 72). By direct observations Yarwood observed the presence of a generative cell [marked 'x' in the figure] elongating and dividing to produce a conidium initial at the apex and a lower cell that retains its generative capacity.

When Mason and Hughes (Hughes (47)) made the combination *Coniosporium peziza* (Cooke & Ellis) (≡ *Sporidesmium peziza* Cooke & Ellis) they were wrong. The conidia in this fungus are in basipetal chains and the fungus is a *Sirodesmium*, hence **Sirodesmium peziza** (Cooke & Ellis) Mason & Hughes comb. nov.*

In *Coniothecium betulinum* Corda (see below) a section through a pustular fructification shows the conidia to be finally dictyospores and they develop in basipetal chains from more or less undifferentiated hyphae of the semi-immersed stroma.

In *Trimmatostroma salicis* Corda, the type species of this genus, the fructifications are pustular as in the foregoing. The conidia arise in basipetal chains from more or less undifferentiated hyphae of the semi-immersed stroma. This genus is usually classified amonst the phragmosporae but a number of conidia will be seen to possess one or more longitudinal septa. I do not understand how *T. salicis* and *Coniothecium betulinum* can be held in different genera, to say nothing of different groupings. In both species no acropetal conidia develop but branched chains occur in both, especially in *Trimmatostroma salicis* where the origin of a branch is often at a triradiate conidium or at a conidium bearing a short lateral outgrowth at right angles usually and in no

* ≡ *Sporidesmium peziza Cooke & Ellis in Grevillea, 4 : 178. 1876.*

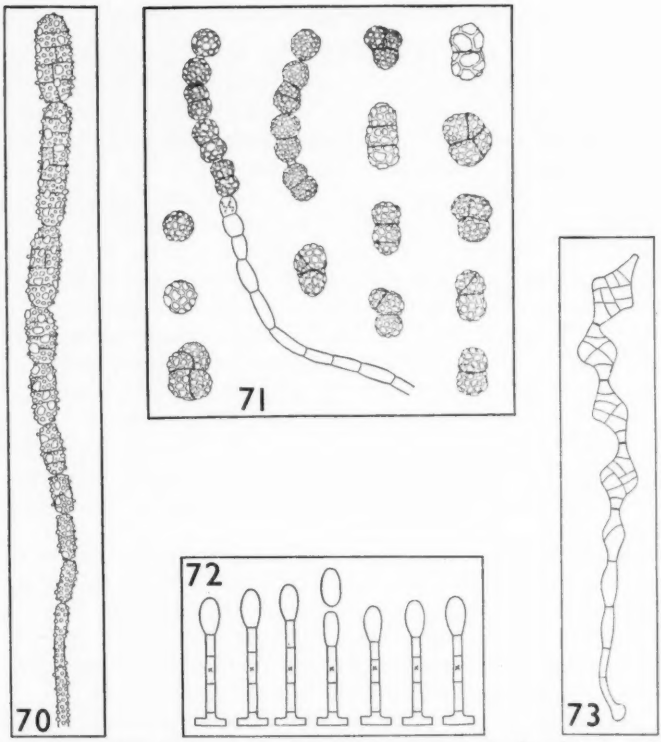


FIG. 70. *Hysterium insidens*, isolated conidiophore and chain of conidia from Hughes (64); ×500.

FIG. 71. *Sirodesmium diversum*, conidiophore and conidia from Hughes (64); ×500.

FIG. 72. *Erysiphe polygoni*, development of conidia from Yarwood (117); reduced from original.

FIG. 73. *Phragmotrichum chailletii*, conidiophore and conidia from Reliq. Farl. no. 665 on *Abies*; ×500.

regular position with regard to the linear part of that particular conidium. I believe the lateral branches have arisen by a lateral (as well as a longitudinal) swelling of a conidium initial; septation is followed by the longitudinal expansion of one cell and the lateral expansion of the other to produce a basipetal chain similar to the main chain on which it is borne.

In *Coniothecium atrum* Corda (22), the type species of the genus, the conidia were described as embedded in slime and one of the illustrations is described thus: 'Sporenhaufschen in Wasser zerfliessend, und die braune Gallerte und die Sporen.' Eleven species classified subsequently by Corda in *Coniothecium* seem to have little in common with the type species. *C. betulinum* is one of these; in Herb. DAOM the collections of this species are disposed as **Trimmatostroma betulinum** (Corda) comb. nov.*

* ≡ *Coniothecium betulinum Corda in Icones Fungorum, 1 : 2. 1837.*

It is interesting to note that most *Sirodesmium* spp., *Trimmatostroma salicis*, and *T. betulinum* produce pustules of dry phaeospores.

In DAOM 29327 and the collections issued in Reliquiae Farlowianae no. 200*a*, *b*, sub *Stilbum glomerulisporum* Ell. & Everh. [nomen nudum], the white or cream colored fructifications may be tuberculariaceous or stilbaceous. The conidia arise in basipetal succession from single or from two neighboring cells of conidiophores which possess a generative region towards the apex. The mature dictyosporous or bulbil-like hyaline conidia are composed of adpressed and coiled outgrowths of the initial cells; they remain in long chains even in teased preparations and the individual conidia are often separated the one from the other by one or two unchanged cells of the hypha from which they have developed. The fungus is not a *Stilbum* but I know of no generic name wherein it can adequately be classified when it is described.

It appears that this type of conidium development is to be found amongst fungi classified in the Coelomycetes. In the pycnidia of the European *Alysisporium rivoclarinum* Peyronel (97) the pycnospores were figured as arising in basipetal succession with a very gradual transition from pycnospore initials to mature pycnospores. Furthermore they are held apart at maturity by a hyaline disjunctor (compare with conidial *Hysterium insidens*) and it seems very probable that the type of development in Peyronel's species is similar to that which is characteristic of Section V. In *Phragmotrichum chailletii* Kunze (Fig. 73) there is a basipetal succession of conidia as in the conidial chains of *Sirodesmium* and their gradual maturation is readily observable in sections through the fructifications.

In the 'Melanconiaceous' fungus described and figured in Grove (41) as *Septotrullula bacilligera* var. *cambrica* Grove & Rhodes the conidia arise in basipetal chains and show a gradual maturation. A large number of genera of the Coelomycetes (Sphaeropsidales, Melanconiales) are described with spores in chains; it seems to me to be essential to know exactly how the chains arise; I know of no pycnidial fungus in which the pycnospores arise in acropetal succession.

The gradual basipetal maturation of the conidia suggests that food material passes up the chain of developing initials. The conidia are in true chains.

Section VI

The main character possessed by species being included in this section is the apparent development of solitary conidia at minute, single, or numerous pores in the wall of the conidiophore. The effect of this on the apex of the conidiophore or wherever such conidia are produced and the base of the conidium is very striking. The apex of the conidiophore is nearly always rounded and the outer and inner walls come to an end abruptly thus delimiting a more or less cylindrical pore. The base of the conidium is also usually rounded and a morphological scar such as a conspicuous tear or break in the wall is absent; the base of the conidium may be truncate but nevertheless the outer wall of the conidium is continuous all round the base except for the basal pore.

The torn outer wall such as found in conidia of Sections I, II, and III for instance is absent. In some of the conidia produced in Section III the scar may be visible as a flat and thickened area at the base of the conidium; such clearly demarcated and thickened areas are not found in the conidia of Section VI. It is necessary to mention at the outset that I have found the main character of Section VI to be a difficult one but, for all that, I believe that it brings together fungi to form a homologous group of very closely related genera; the need for further morphological studies in this group is stressed.

In some species the conidiophore is simple and the apical conidium checks all further growth. Lateral conidia, however, may develop in verticils below the uppermost septa or irregularly along the length of the conidiophore and in such cases chains of conidia may occur. These lateral conidia, like the apical ones, fall readily from their attachment and although darker colored areas on the conidiophore marking the point of their insertion may be completely absent, the seat of their former attachment can easily be located by the presence of the minute pores.

In *Exosporium tiliae* Link ex Wallr. (Fig. 74), for instance, the apex of the conidiophore is rounded and shows the pore clearly; in a young collection a conidium initial makes its appearance as a minute hyaline bulb at the pore

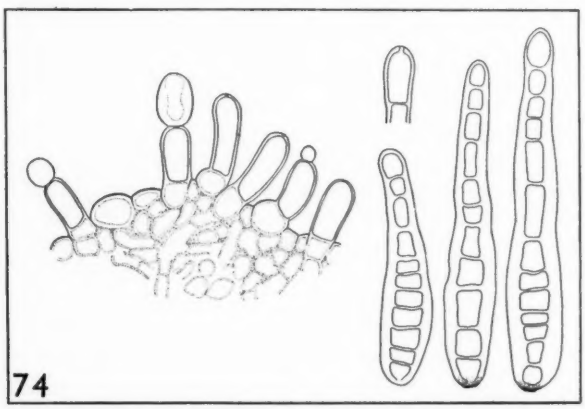


FIG. 74. *Exosporium tiliae*, conidiophores and conidia (I.M.I. 6787); ×500.

just as if it had resulted from a blowing out of the inner wall of the conidiophore. During further development the initial increases in length and width and its base comes to lie over a part of the rounded apex of the conidiophore but in no instance can I observe direct continuity between the outer wall of the conidiophore with that of the conidium. In *E. tiliae* and some species of *Helminthosporium* (sensu stricto) the base of the conidium, more especially the terminal ones, is dark brown and turbinate. The conidiophores are minute in *Exosporium tiliae* and cover the surface of large superficial hemispherical stromata; only solitary conidia develop on these conidiophores. The only

other true *Exosporium* spp. known to me are *E. biformatum* v. Höhn. which I collected on *Fagus sylvatica* wood (the type host) in England (I.M.I. 10912 (*b*)), and *E. cespitosum* Ell. & Barth.

In *Helminthosporium velutinum* Link ex Fr., the type species of *Helminthosporium*, the conidia develop terminally and in more or less regular verticils below the terminal conidium and below the uppermost septa (Fig. 75) of the subulate conidiophore.

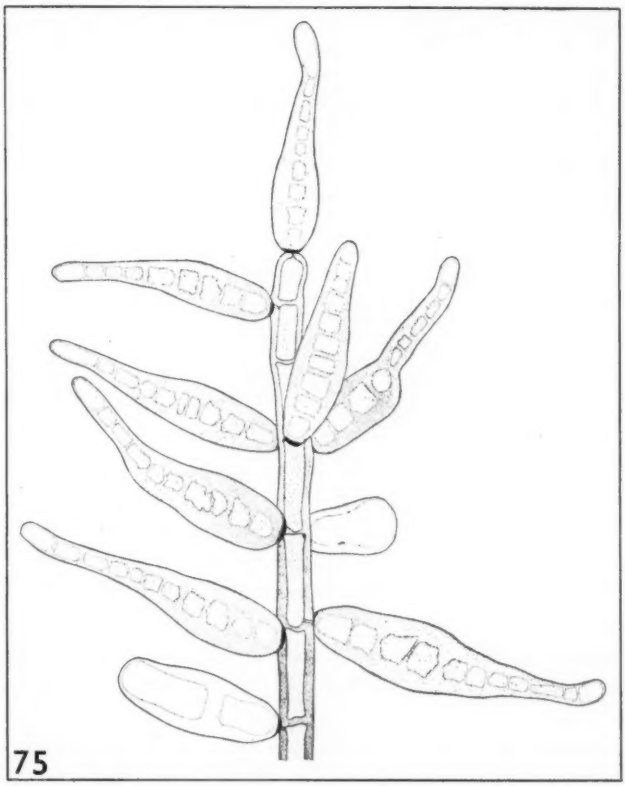


FIG. 75. *Helminthosporium velutinum*, apex of conidiophore with conidia from pure culture (I.M.I. 349(*a*)); ×500.

In **Helminthosporium atrovirens** (Harz) Mason & Hughes comb. nov.*, (Fig. 76) well known as the cause of silver scurf of potato tubers, the conidia develop exactly as in the type species of *Helminthosporium* and the new combination becomes necessary.

* ≡ *Spondylocladium atrovirens Harz in Bull. Soc. Imp. Moscow, 44 : 42. 1871.*

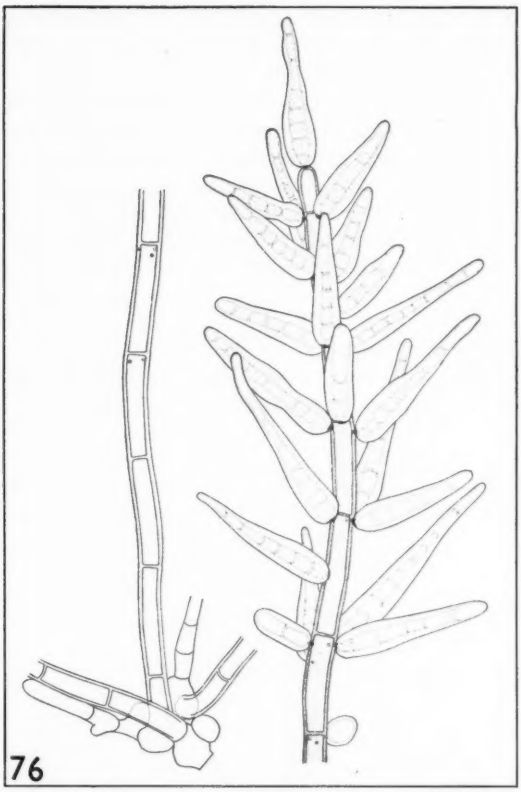


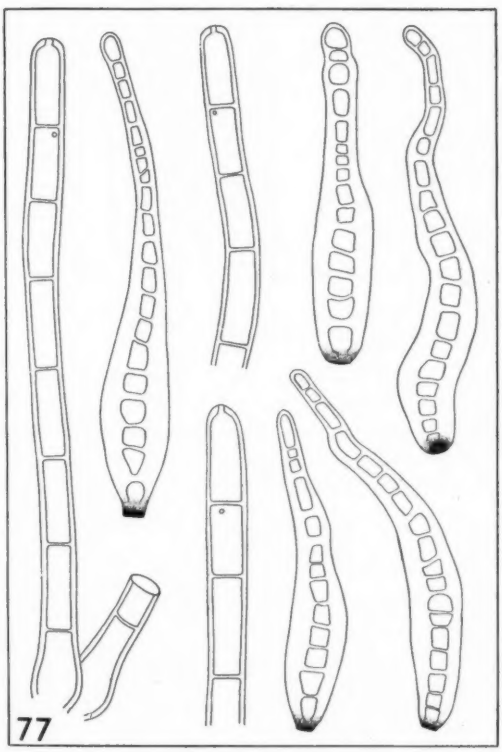
FIG. 76. *Helminthosporium atrovirens*, conidiophore and conidia (I.M.I. 1685); ×500.

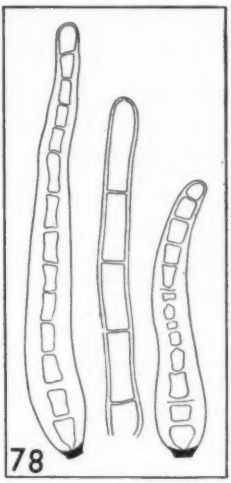
In *H. microsorum* D. Sacc. (Fig. 77) conidiophores are in tufts on dead twigs of *Quercus ilex*; they bear a terminal conidium and one or two lateral conidia as well.

'*Helminthosporium tiliae* Fr.' is very similar to *H. microsorum* but the conidiophores bear only solitary terminal conidia (Fig. 78).

An unidentified *Massaria* (I.M.I. 19472(*a*, *b*)) on *Quercus* grew in association with a *Helminthosporium*; conidiophores and conidia of the *Helminthosporium* developed from ascospores in pure culture. As far as I am aware this is the first time that a true *Helminthosporium* has been connected with a perfect state.

In *Helminthosporium smithii* Berk. & Br. (Fig. 79) solitary conidia are produced at the apex of conidiophores which may then proliferate through the apical pore and form another conidium at the apex of the proliferation; two





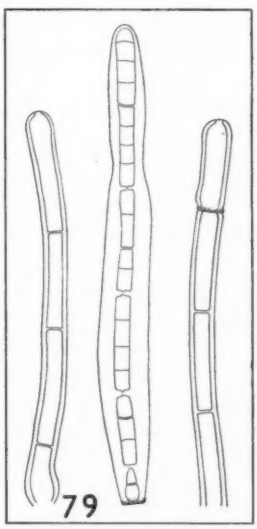


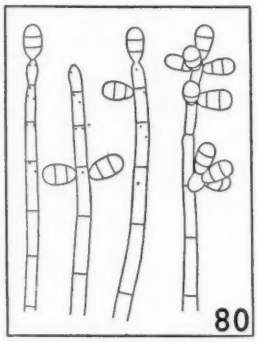
FIG. 77. *Helminthosporium microsorum*, conidiophores and conidia (I.M.I. 19654); ×500.

FIG. 78. *'Helminthosporium tiliae'*, conidiophore and conidia (I.M.I. 9070); ×500.

FIG. 79. *Helminthosporium smithii*, conidiophores and a short conidium (I.M.I. 31422); ×500.

or three such proliferations have been seen. This, of course, is characteristic of *Corynespora cassiicola* (Berk. & Curt.) Wei (113) which may also form short acropetal chains of conidia.

In **Spondylocladium obovatum** (Cooke & Ellis) comb. nov.* (Fig. 80) a not uncommon Eastern North American Hyphomycete of rotten wood and bark the conidiophore bears irregular lateral whorls of conidia which leave characteristic pores after seceding. The terminal conidium, however, arises obviously as a blown-out end of the apex of the conidiophore but a further note on this apparent anomaly is given on p. 640.



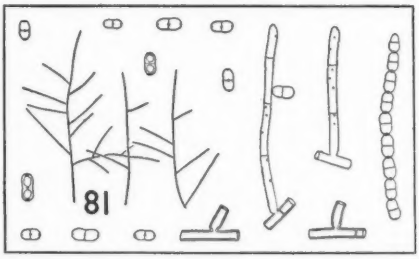


FIG. 80. *Spondylocladium obovatum*, conidiophores and conidia (DAOM 29394(*a*)); ×500.

FIG. 81. *Diplococcium spicatum*, conidiophores and conidia (I.M.I. 27623); ×500 except low power outlines of entire conidiophores which are ×50.

In *Diplococcium spicatum* Grove (Fig. 81), the type species of *Diplococcium*, the main stalk of the conidiophore is erect, more or less straight, and it bears up to nine 'lateral branches' which form a wide angle with the main stalk; these may themselves bear upwardly directed laterals. Along the terminal portion of the main stalk and along the length of the lateral branches are found minute scattered pores which denote the place of the former attachment of long, fragile, acropetal chains of subhyaline didymospores.

In **Diplococcium uniseptatum** (Berk. & Curt.) comb. nov.** the simple conidiophores bear numerous scattered pores at which usually solitary, brown, 1-septate, readily seceding conidia are borne.

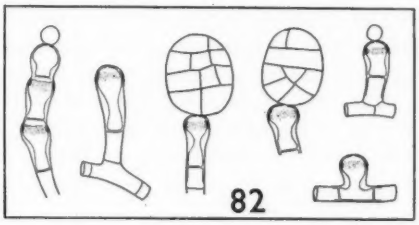
In **Diplococcium indivisum** (Sacc.) comb. nov.† a common mold of wood and bark around Ottawa, Ont., and Ithaca, N.Y., the simple conidiophores bear numerous scattered pores at which solitary, brown, continuous conidia develop.

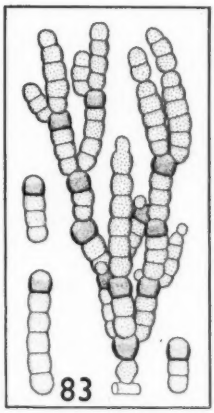
In the *Stemphylium* conidial apparatus of *Pleospora herbarum* (Pers. ex Fr.) Rabenh. (see Wiltshire (116)) and in *Stemphylium sarcinaeforme* (Cav.) Wiltshire (116) (Fig. 82) solitary conidia are produced on branched or unbranched conidiophores which proliferate through the pore left by one

* ≡ *Acrothecium obovatum Cooke & Ellis in Grevillea, 5 : 50. 1876.*

** ≡ *Virgaria uniseptata Berk. & Curt. apud Berk. in Grevillea, 3 : 145. 1875.*
≡ *Cladotrichum uniseptatum (Berk. & Curt.) Sacc. in Sylloge Fungorum, 4 : 373. 1886.*
= *Cladosporium aterrimum Ell. & Everh. in Proc. Acad. Phil. 1894 : 378. 1894.*

† ≡ *Virgaria indivisa Sacc. in Michelia, 2 : 560. 1882.*





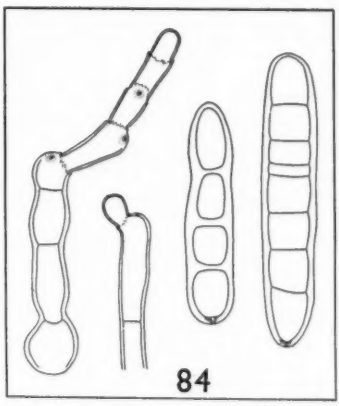


FIG. 82. *Stemphylium sarcinaeforme*, conidiophores and conidia (DAOM 14970); ×500.

FIG. 83. *Torula herbarum*, conidiophore, conidial chains, and conidia (I.M.I. 15281); ×500.

FIG. 84. *Helminthosporium teres*, conidiophores and conidia (DAOM 1056); ×500.

conidium and then produce another conidium at the apex of the proliferation. Occasionally the proliferation will be just lateral to the apical conidium which remains attached.

In *Torula herbarum* Link ex Fr. (Fig. 83) terminal cells of the conidiophore are not unlike those of *Stemphylium* prior to proliferation; in *T. herbarum*, however, up to three conidia may be borne on the end cell of the conidiophore and branched acropetal chains of phragmospores develop. The apical cell of each conidium within the chain is usually characteristically darkened and thickened like the terminal cell of the conidiophore.

In '*Helminthosporium teres*' Sacc. (Fig. 84) the first conidium is terminal. Then the conidiophore develops a growing point just below the apex and if the outer wall of the conidiophore has hardened then the inner wall bursts through it, grows upward, and displaces the pore left by the apical conidium, and then produces another terminal conidium. A succession of such new growing points arises in this way so that the once terminal pores become lateral in position. The apex of the conidiophore and the base of the conidium are similar in possessing a pore and furthermore, within each apical and basal

cell of conidiophore and conidium respectively, just below (or above) the pore is a brown ring which gives a characteristic appearance in side view. A thickened hilum as often found in Section III is not seen here. In some graminicolous species assigned to *Helminthosporium* the base of the conidium may be truncate just as in some conidia of *H. velutinum* and related species.

The production of successive conidia in *Curvularia* spp. e.g. *C. lunata* (Wakker) Boedijn (Fig. 85) is similar to that found in *Helminthosporium teres* Sacc.

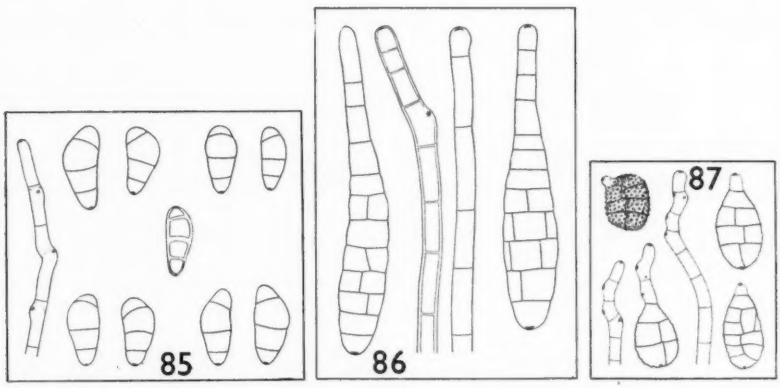


FIG. 85. *Curvularia lunata*, conidiophore and conidia (DAOM 14976); ×500.
FIG. 86. *Alternaria brassicae*, conidiophores and conidia (DAOM 14161); ×500.
FIG. 87. *Alternaria consortiale*, conidiophores and conidia (DAOM 14937); ×500.

In *Alternaria* spp. solitary or acropetal chains of conidia develop on conidiophores which may or may not increase in length with further conidium production. In *A. brassicae* (Berk.) Sacc. (Fig. 86) chains of conidia and increase in length of the conidiophore occur apparently only in pure culture. In **Alternaria consortiale** (Thüm.) Groves & Hughes comb. nov.* (Fig. 87), on the other hand, chains of conidia are not infrequent and the conidiophore may become markedly geniculate following the development of successive new growing points each terminating in a single conidium or a chain of conidia.

In *Dendryphion comosum* Wallr., the type species of Wallroth's genus, the growth of the erect main stalk of the conidiophore is usually terminated by a conidium which then develops an acropetal chain of similar conidia. In the meantime lateral branches, often in whorls, have arisen below the apex and these are also branched and bear acropetal chains of conidia.

In *Dendryphion laxum* Berk. & Br. (Fig. 88) the branching of the conidiophore is not usually so pronounced; the lateral branches produced, usually below the terminal conidial chain, produce a succession of subterminal growing

* ≡ *Macrosporium consortiale Thüm. in Herb. myc. oecon. no. 450. 1876.*
≡ *Stemphylium consortiale (Thüm.) Groves & Skolko in Can. J. Research, C, 22 : 196. 1944.*

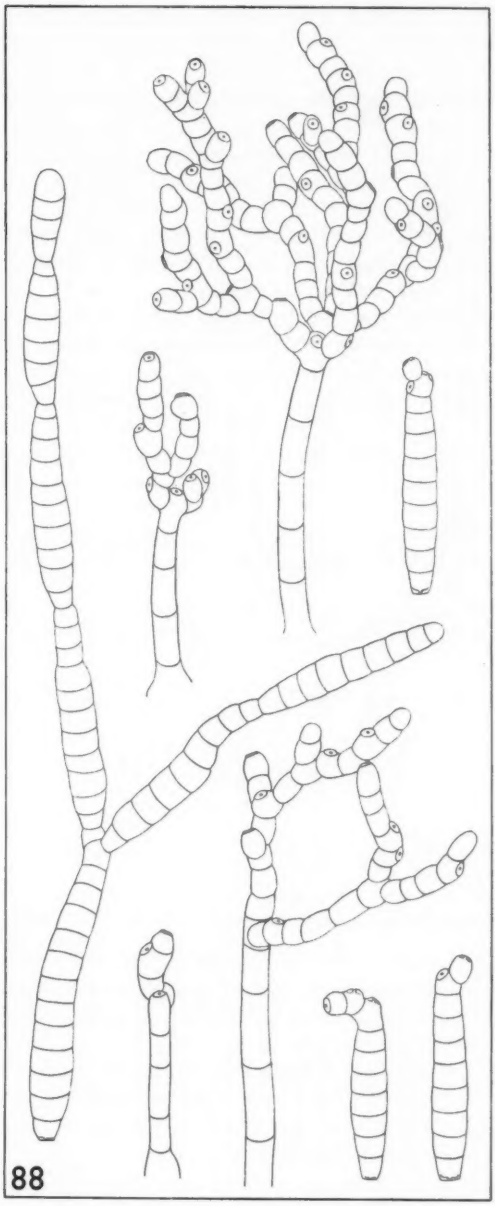


FIG. 88. *Dendryphion laxum*, conidiophores and conidia (I.M.I. 4133); ×500.

points each terminating in an acropetal chain of phragmospores. The chains may be branched and the apex of a conidium may proliferate like the apex of one of the lateral branches.

In **Dendryphion interseminatum** (Berk. & Rav.) comb. nov.* the branching of the conidiophore is not so localized as in the preceding species; the conidiophores are nodulose indicating where a number of conidia have arisen. The conidia are usually formed in short acropetal chains. The genus *Dendryphiella* is based on this species and I see no reason for holding this distinct from *Dendryphion* merely on account of the looser and longer branches. The catenulate conidia have basal and apical pores and the point of attachment of conidia to the conidiophores is also marked by a pore. The fungus can be excluded from *Heterosporium*, on account of the method of conidium development; in this paper *Heterosporium* is included in Section II.

In the next genus described, a solitary conidium terminates the growth of the main stalk of the conidiophore; primary, secondary, tertiary, and even quaternary distinct lateral branches arise each in turn being terminated by a solitary conidium. In *Dendryphiopsis atra* (Corda) Hughes (Figs. 89, 90, see also p. 655) the main stalk retains that form which it reached at the formation of the apical conidium. Lateral branches arise by bursting through the outer wall of the conidiophore, develop apical conidia, and a dichasium-like head is the result. Corda (25) figured long chains in this species but an authenticated (possibly type) collection shows only solitary conidia. *D. atra* is one of the commonest wood and bark hyphomycetes of the Ottawa district and is equally common around Ithaca, N.Y. It has received at least one independent name in North America.

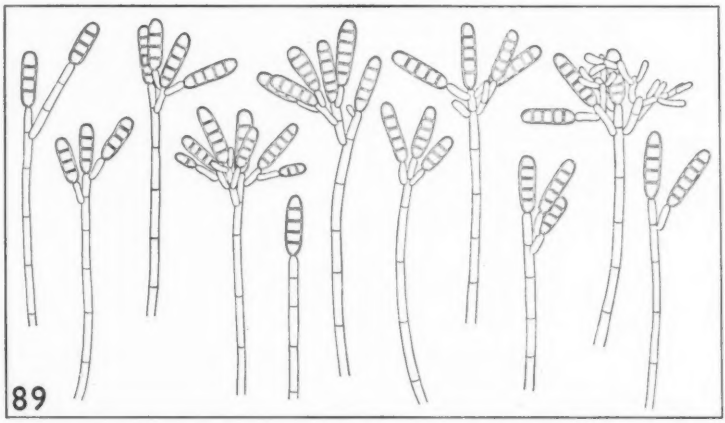


FIG. 89. *Dendryphiopsis atra*, conidiophores and conidia (I.M.I. 4493); ×165.

* ≡ *Helminthosporium interseminatum Berk. & Rav. apud Berk. in Grevillea, 3 : 103. 1875.*
≡ *Dendryphiella interseminata (Berk. & Rav.) Bub. & Ran. in Ann. Mycol. 12 : 417. 1914.*

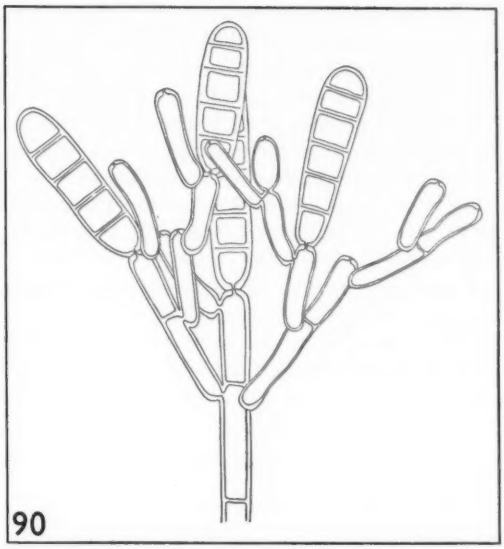


FIG. 90. *Dendryphiopsis atra*, conidiophore and conidia (I.M.I. 4493); ×500.

In '*Helminthosporium stemphylioides* Corda' (≡ *Brachysporium stemphylioides* (Corda) Sacc.) (Fig. 91) the scattered conidiophores are inflated at the

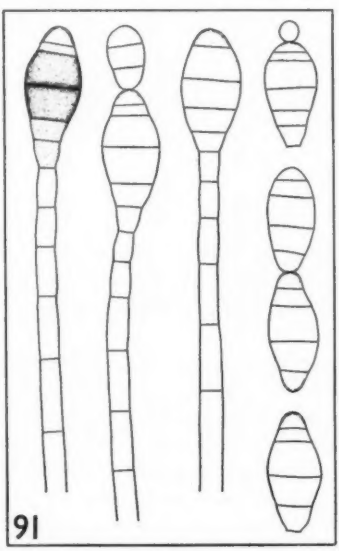


FIG. 91. '*Helminthosporium stemphylioides* Corda', conidiophores and conidia (I.M.I. 19219(*j*); ×500.

apex into conidium-like structures which may secede at maturity but apparently with difficulty. Before seceding, however, each of these will have borne at its apex a single unbranched chain of conidia whose development necessitates the classification of this fungus in Section VI. It will be remembered that the apical conidium of *Spondylocladium obovatum* (Fig. 80) is a blown-out end of the conidiophore and is more persistent than the lateral ones which develop as in *Helminthosporium velutinum.*

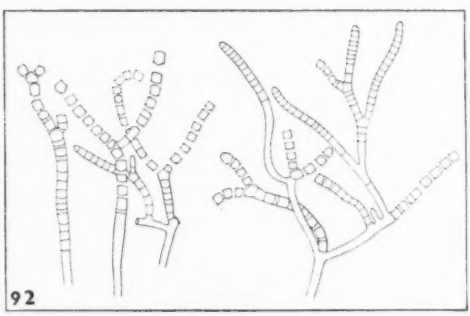
In 1951 Hughes (53) suggested that the four-armed conidia of *Tripospermum eggelingii* Hansf. might have developed at pores. No further material of this or congeneric species has been seen.

Admittedly the character used in delimiting Section VI may be a difficult one but it is extremely evident in large numbers of species which have other characters in common; many have determinate conidiophores and a characteristic conidial shape and structure. I feel that a useful purpose is being served in drawing attention to this type of development by basing a Section on it.

Section VII

In this section are classified those species whose conidia arise from the septation and breaking-up of simple or branched hyphae.

In **Coremiella ulmariae** (MacWeeney) Mason comb. nov.* (Figs. 92, 93) the conidiophores are in tufts and each grows apically and branches irregularly



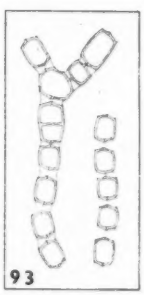


FIG. 92. *Coremiella ulmariae*, conidiophores (I.M.I. 8977); ×315.
FIG. 93. *Coremiella ulmariae*, portions of chains of conidia (I.M.I. 8977); ×750.

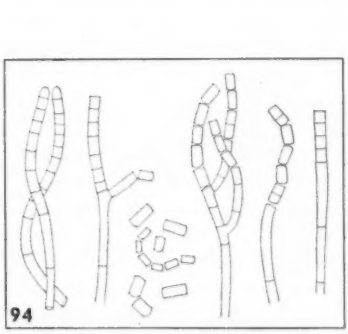
or somewhat dichotomously to become arborescent towards the apex. Transverse septa are laid down in basipetal succession in the upper branches and neighboring or alternate cells develop thicker walls, a process which also takes place basipetally. The intermediate cells lose their contents entirely and the lateral walls remain thin, collapse inwards, and finally break readily to free the oblong or cubical conidia. The conidium it will be realized has developed

* ≡ *Stysanus ulmariae McWeeney in Irish Naturalist, 4 : 277. 1895.*
The genus Coremiella was published by Bubák & Krieger (Bubák (18)) for the single species C. cystopoides which they illustrated.

within the outer wall of the original hypha and the characteristic papilla and minute pore of the end walls are clearly visible; conidia which have seceded show a minute frill at each end, this being the remains of the outer wall, of the original hypha belonging to one of the collapsed cells. Only the terminal branches of conidiophores become modified into conidia.

In *Geotrichum* sp. (DAOM 29164, Fig. 94) more or less undifferentiated, simple or branched, hyaline hyphae develop septa in basipetal succession; each cell becomes thicker-walled and secedes by the breaking down of the outer wall and a separation of the transverse wall which is presumably a double structure. The conidia are hyaline and oblong at maturity but yellow in mass in this particular isolate.

Langeron (76) has illustrated *Geotrichum candidum* Link ex Sacc. and also reproduced a figure by Arnaud and Barthelet (2) of *G. purpurascens* (Bon.) Sacc., both species producing conidia in the manner described here.



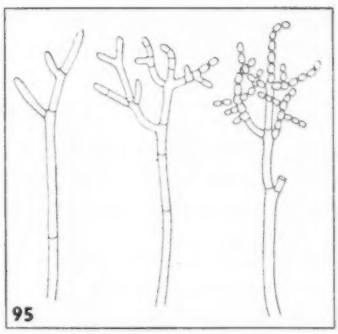


FIG. 94. *Geotrichum* sp., conidiophores and conidia (DAOM 29164); ×750.
FIG. 95. *Oidodendron griseum*, conidiophores with branched apices at various stages of development and fragmentation, from pure culture (I.M.I. 45947); ×750.

In *Oidiodendron griseum* Robák (98) the more or less well differentiated pale brown main stalk of the conidiophore branches irregularly towards the apex and finally septates basipetally, the cells becoming rounded off, slightly roughened, and colored (Fig. 95). At maturity the conidia fall very readily leaving the erect main stalk of the conidiophore with the stumps of former branches at the apex.

Such a breaking-up of hyphae into conidia is seen in *Hendersonula toruloidea* Nattr. (Nattrass (90) and Hughes (59)). On *Manihot utilissima* the fungus forms blister-like swellings under the periderm and these are filled with conidia which have developed in this manner. The formation of conidia can be well studied in pure culture on agar media.

Brodie (16) described the formation of 'oidia' by *Coprinus lagopus* (Fr.) Fr. Normal 'oidiophores' have an erect stalk with a sparingly branched apex bathed in a drop of liquid; the apical branches segment basipetally into the 'oidia'. This is reminiscent of *Oidiodendron* but here the conidial heads are dry.

Brodie (17) also described the basipetal formation of uninucleate 'oidia' in *Collybia velutipes* (Curt. ex Fr.) Quél. by the successive division of the single nucleus of a hypha and the successive segmentation of that hypha. Chains of conidia so formed usually separate in water. This type of development from a more or less undifferentiated hypha is reminiscent of *Geotrichum*.

Kaufert (73) illustrated and described the production of binucleate and uninucleate conidia from coremia on 'dicaryotic' and 'haploid' mycelia respectively of *Pleurotus corticatus* Fr. The conidia are yellow-brown and are formed in a liquid resulting in glistening black masses. The free ends of the hyphae at the tips of the coremia were stated to break up 'in a basipetal manner into chains of conidia'. Such synnemata (coremia) are reminiscent of *Coremiella*, but in the type species of this genus the conidia are dry.

Drechsler (31) illustrated and described 18 species of *Actinomyces*; he stated that 'sporogenesis commences at the tip by the insertion of regularly spaced septa, and proceeds downward towards the base of the filament'; such filaments are frequently spiral. The method of conidium development by basipetal fragmentation certainly suggests that *Actinomyces* should be included in Section VII.

Section VIII

In this section are included those species whose conidiophores elongate by a basal growing point. The conidiophore itself may arise from a barrel-shaped or flask-shaped conidiophore mother-cell which usually bears a terminal, often atypical conidium prior to development of the conidiophore. The conidia of mature conidiophores are either borne solitarily at the apex or apically and irregularly on short stalks along the increasing length of the conidiophore, or apically and in whorls between thickened septa of the conidiophore. All the conidia arise as blown-out ends and the oldest conidia are usually towards the apex and the youngest towards the elongating base of the conidiophore.

The various species produce fructifications which are usually pustular, superficial, and with dry powdery conidia. The conidia are mostly colored and may be amerospores or septate in such a way that the conidia are composed of a flattened or irregular plate of 4, 8, or 16 cells. The amerospores are usually flattened, almost lenticular and bivalvate with a longitudinal germ slit. Mason (82) proposed the tribe 'bivalvae' to contain such genera as *Papularia*, *Arthrinium*, *Camptoum*, 'and presumably *Pseudocamptoum*'.

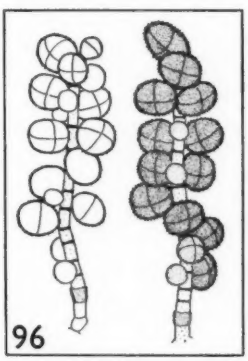
In *Papularia* spp. (see Ellis *et al.* (34) with illustrations) the fructifications may be superficial or immersed and then erumpent. The conidiophores are delicate and hyaline and I consider them to have arisen from conidiophore mother-cells. The first conidium is formed at the apex and subsequent ones are borne laterally on an elongating conidiophore in such a way that the youngest conidia are mostly found towards the base. Mature conidia are more or less circular and bivalvate.

In *Arthrinium* spp. (Ellis *et al.* (34) with illustrations) the conidiophore mother-cells and conidiophores are more or less well developed and with the

conidia form dark brown to black, powdery, superficial, raised fructifications. The conidiophores possess dark brown to black septa between which are borne the angular to bicornate and flattened conidia each with a longitudinal germ slit. The first conidium is terminal and is often abnormal; other conidia arise in succession towards the younger base of the conidiophore although the sequence is often broken by the delayed appearance of some conidia amongst fully formed ones.

In *Endocalyx* spp. (Hughes (68)) the fructifications are semi-immersed; the conidiophores are filamentous and elongate by a basal growing point. The conidia are sessile or shortly stalked and at maturity, flattened, smooth or with ornamentations, continuous, colored, and with a longitudinal germ slit.

In *Dictyoarthrinium* spp. (Figs. 96, 97) (Hughes (59)) the conidiophores possess dark cross-walls and a single terminal, and lateral whorls of conidia borne between the dark transverse septa. The conidia are flattened, rough-



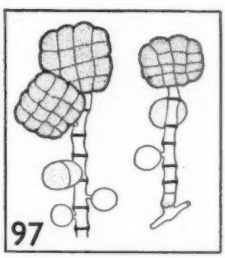


FIG. 96. *Dictyoarthrinium quadratum*, conidiophores and conidia from Hughes (59); ×500.

FIG. 97. *Dictyoarthrinium africanum*, conidiophores and conidia from Hughes (59); ×500.

walled, and quadrately septate; they are four-celled in *D. quadratum* Hughes and composed of a flat plate of 16 cells in *D. africanum* Hughes. The conidiophores elongate by a growing point either within or just above the conidiophore mother-cell and the youngest conidia are generally found towards the base. I observed no germ slits in the conidia of either species. The fructifications are similar to those of *Arthrinium* spp.

In *Spegazzinia tessarthra* (Berk. & Curt.) Sacc. (Fig. 98) and *S. tessarthra* var. *deightonii* (Hughes (68)) the conidiophores arise from conidiophore mother-cells and bear the single terminal conidium prior to elongation. At maturity the conidiophores are of two kinds, micro- and macro-conidiophores, each bearing different kinds of conidia, a single one at the apex of each. The macro-conidiophores are dark brown and do not possess black and wide transverse septa. The conidia of the species and its variety do not possess a germ slit.

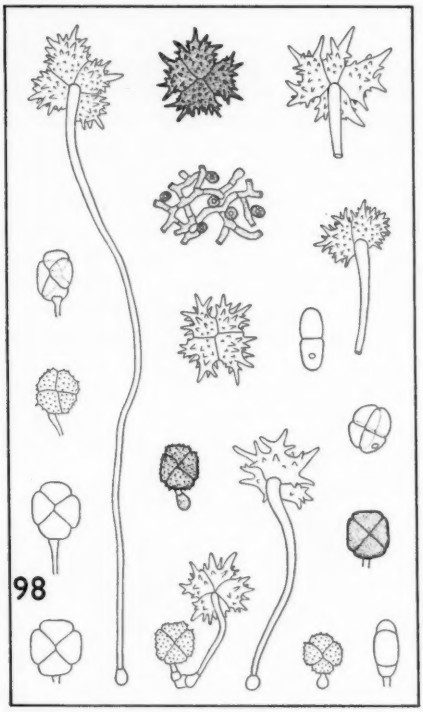
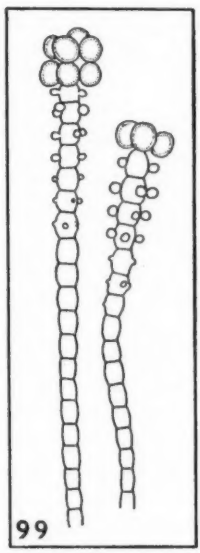


FIG. 98. *Spegazzinia tessarthra*, mycelium, conidiophores, and conidia from Hughes (68); ×500.

(The flattened conidia of *Pseudocamptoum fasciculatum* (Cooke & Massee) Mason have a longitudinal germ slit but this species cannot be classified in this section. In the first place the conidiophores do not arise from conidiophore mother-cells and they elongate by means of a terminal growing point which ultimately blows out into a conidium; a succession of conidia then develops, each conidium being the blown-out end of successively produced growing points just lateral to the previous conidium. *Pseudocamptoum* is classified in Section II.)

Graphiola spp. are currently classified in the *Graphiolaceae* of the Ustilaginales although their location there has always been regarded as dubious. Of *G. borassi* Sydow & Butler (108) the authors stated that the fungus has nothing in common with the Ustilagineae. I believe *Graphiola* spp. such as *G. phoenicis*, *G. thaxteri*, *G. congesta*, and *G. borassi* Syd. & Butl. should be classified amongst the Fungi Imperfecti; these are far more closely related to *Endocalyx* spp. than their usual inclusion in the Ustilaginales would suggest. The illustrations of *Graphiola thaxteri* Fischer (Fig. 99) and *G. congesta* Berk. Rav. by Fischer (38) certainly suggest a basal elongation of the conidio-

phores on which conidia develop laterally apparently in basipetal succession as in *Endocalyx* (Hughes (68)). The illustrations of conidiophores of *G. phoenicis* Poit. (Fischer (37)) are very much like those of *G. thaxteri*. Sydow and Butler's (108) figures (Fig. 100) indicate a basal elongation of conidiophores in *G. borassi*, the individual cubical cells of which develop three to eight linear conidia mostly at the corners; the cubical cells themselves finally secede from each other and presumably function as conidia.



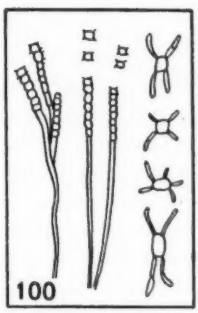


FIG. 99. *Graphiola thaxteri*, isolated conidiophores and conidia from Fischer (38); ×1170.

FIG. 100. *Graphiola borassi*, isolated conidiophores (×486) and conidia (×810) from Sydow and Butler (108).

Discussion

In the preceding pages I have attempted to arrange some Hyphomycetes into sections wherein the types of conidiophore and conidium development and structure are the primary differentiating characters. I believe that these sections show a measure of uniformity including interesting variations on distinct themes which cannot be obtained by using in a major sense the characters employed in the older classifications. Whether this uniformity will be retained by including a far greater number of genera remains to be seen. I have not included the singularly curious type of development of the isthmospores (Hughes (68)) of *Trichothyrium asterophorum* (Berk. & Br.) v. Höhn. and *T. reptans* (Berk. & Curt.) Hughes which develop from and are supported at maturity each by two 'conidiophores'; isthmospores would I believe require to be classified as Section IX. Furthermore, there may well be other types of

conidium development which may not fit adequately into any of the sections delimited. But these data and this classification into major groupings are presented in the belief that a more rational classification in the Hyphomycetes (or Fungi Imperfecti as a whole) will be evolved only when those early stages of conidium development are more clearly understood; such terms as 'budded-off' or 'abstricted' when applied to conidia, without reference to what has actually happened or is actually happening to the conidiophore, do not seem to help very much.

I hope this paper will stimulate not criticisms alone but criticisms accompanied by details of early conidium development more definite than have appeared in the past.

Whereas a large number of well or poorly differentiated terms are available for various spore forms the reverse seems to be true for 'conidiophores'. This term has been used very loosely in the above account but the need for more precise terms is evident. In *Dendryphiopsis* and *Verticicladium*, for instance, when the main stalk and branches are referred to as branched conidiophores it does not specify any distinctive type of compound lateral branches borne on a main stalk. The term conidiophore can be used satisfactorily only for simple conidia-bearing structures.

In mononematous and synnematous fructifications the actual structures bearing the conidia may be well differentiated. The *phialide* can I believe have a precise meaning and implies a unicellular structure. The term *annellophore*, however, can apply to the long multiseptate conidiophore of *Annellophora* as well as to one of the annellated sporogenous cells of *Stysanus* and I believe a distinction needs to be drawn. In Section II conidia develop in the same way on the long multiseptate conidiophore of *Virgariella* as they do on one of the ultimate unicellular sporogenous cells of a *Verticicladium* or *Costantinella* fructification; in the last named it will be remembered that the unilateral, linear, close succession of conidia led to the term 'cervix' but as far as I am aware this can only be used for two (and a possible third) species of *Costantinella*. No precise term for the conidiophore or sporogenous cell of Section II have been proposed but such a term would greatly facilitate the description of many Fungi Imperfecti. The terms acrogenous and acropleurogenous can be used equally well for a few distinct types of conidiophores. Furthermore, there seem to be no terms available to indicate precisely the characters of conidiophores of Sections I, V, VI, VII, or VIII.

A number of interesting examples of outward similarity between fructifications in the various Sections occur. For instance slimy heads of hyaline amerospores on mononematous, dematiaceous conidiophores are produced by *Haplographium*, *Verticicladiella*, *Leptographium*, and *Hantzschia* but conidium development is different in all four and necessitates their segregation into Sections I, II, III, and IV respectively. Furthermore a comparison of the following is interesting: *Calcarisporium* [II] and *Verticillium* [IV]; *Gonatobotrys* [I] and *Arthrobotrys* [II]; *Heterosporium* [II], *Cladosporium* [I], and

Oidiodendron [VII]; *Spilocaea* [III] and *Fusicladium* [II], to mention only a few examples of parallelism involving distinct types of conidium development.

Nuclear behavior during conidium production has been neglected. The nuclear phenomena during conidium (oidium) production, by the method of Section VII, in *Collybia velutipes* have been described by Brodie (see p. 642). Some further examples are included here.

Nobles (92) stated that in *Peniophora allescheri* (= *P. mutata* (Peck) v. Höhn. & Litsch. fide Dr. Nobles, personal communication) successive division of the single nucleus in the oedocephaloid conidiophore head resulted in 2, 4, 8, 16, or more nuclei. 'The nuclei take up their positions around the inner surface of the distal half of the conidiophore. . . . . At this stage the slender tapering sterigmata push out and a swelling, the developing conidium, appears on the end of each. While the spore is still small a nucleus migrates into it. . . . . '. Uninucleate conidia in the oedocephaloid conidiophores of *Corticium effuscatum* Cooke & Ellis were shown to arise in a manner similar to the aforementioned (Nobles (93)).

Constance Loveland (unpublished researches) informs me that a similar behavior of the nuclei is seen in *Botrytis* spp. In *B. allii* single nuclei migrate into the conidium initials and divide once so that the conidia are binucleate. In *B. cinerea* and *B. streptothrix* (Cooke & Ell.) Sacc. a number of nuclei migrate into each conidium initial from the ampulla on which the conidia develop. I know of no publications dealing with nuclear phenomena in any of the other species included in Section I and which do not show such a simultaneous development of conidia.

Biggs (8) described and illustrated the successive sympodial production of conidia [as 'oidia'] in cultures of *Corticium coronilla* v. Höhn. & Litsch. Of interest is the demonstration of successive divisions of the nucleus of the conidiophore [as 'oidiophore']; one of the daughter nuclei passes to the tip of the growing point which is cut off as a conidium whilst the other divides again and one of the daughter nuclei then passes to the tip of a new growing point which has developed to one side of the base of the previous conidium. This process is repeated a number of times. This method of conidium production is characteristic of Section II but details of nuclear behavior in any other members are unknown to me. It would be extremely interesting to know the nuclear content and behavior in say *Arthrobotrys* spp. during development of conidia (see p. 599).

Backus and Keitt (4) studied nuclear phenomena in *Venturia inaequalis* and found the cells of the vegetative mycelium, conidiophore, and conidium to be uninucleate. It would appear from their illustrations that a daughter nucleus resulting from the division of the conidiophore nucleus migrates into the conidium initial which is then cut off by a cell wall. This is similar to the method described by Biggs (8) except that the successive conidia in *V. inaequalis* are produced by successive proliferations *through* the old scar (Section III). I find no reference to similar work on *V. pirina* Aderh. which produces conidia as in Section II.

Martens and Vandendries (80) described and illustrated three types of accessory spores in *Pholiota aurivella* Batsch. Their semidiagrammatic illustrations are reproduced here as Fig. 101 in which *A* shows 'oidiophores' with basipetal segmentation into 'oidia', the main stalk being terminated by a 'chlamydospore'; *B*, shows a solitary terminal 'chlamydospore' and *C*, fusiform conidia arising successively at the apex of a conidiophore by the blowing out of successive new growing points. In this fungus, therefore, we find three types of conidium development as characteristic of Section II (Fig. 101 *C*), Section III (Fig. 101 *B*), and Section VII (Fig. 101 *A*).

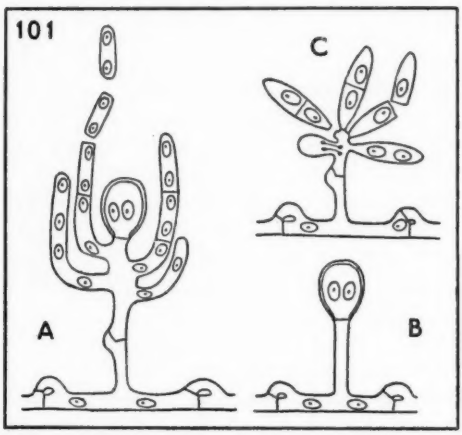


FIG. 101. *Pholiota aurivella*, conidiophores and conidia from Martens and Vandendries (79); slightly reduced from original.

As stated on p. 580 the term 'conidium' has been used in all Sections except IV. But some of the terms proposed by Vuillemin and Mason may be usefully applied to some of the 'conidia' of the other Sections.

Section I.—Because of developmental similarity between say the *Oidium* fructifications of *Pellicularia pruinata* and the fructifications of *Cladosporium* the two parts A and B of Section I were at first combined. The result was a heterogenous group. More uniformity in both Sections was obtained by separating into A those species with predominantly narrow mycelial hyphae and into B those with predominantly wide mycelial hyphae.

In Section IA the conidia are nearly always in chains; they are '*blastospores*' (arising as globular buds or blown-out ends) and their development in acropetal chains is inferred by this term.

In Section IB the conidia are very commonly solitary and I call them *solitary blastospores*; when they occur in botryose clusters the conidia are *botryose solitary blastospores* as in *Botrytis* and *botryose blastospores* in *Gonatobotryum* or *Nematogonium* in which fungi the conidia are in chains. The conidia in this Section are nearly all dry.

Section II.—The conidia are '*terminus spores*'; in many instances, e.g., *Ramularia* and *Heterosporium*, the terminus spores may bud at the apex and produce *blastospores* but in the chains produced the basal or primary conidium is a terminus spore. In *Arthrobotrys* the conidia may develop in clusters and such conidia may be described as *botryose terminus spores*. Terminus spores are nearly always dry, but produced in slime in a few instances.

Section III.—The conidia are '*chlamydospores*' and are usually produced at the apex of a hypha; they are solitary and usually large, thick-walled, and dark colored but may be small, hyaline, and not particularly thick-walled especially when developing in slimy heads. It will be remembered that intercalary chlamydospores occur in many fungi and both terminal and intercalary chlamydospores may be produced by the same fungus. When chlamydospores are terminal, annellations may be produced on the conidiophores (*annellophores*) and *successive chlamydospores* may remain loosely attached in chains.

The disadvantage of the character implicit in the term annellophore is the great difficulty that may be encountered in observing the actual annellations more especially in those species whose annellophores are narrow and hyaline. Nevertheless it seems to be such a well established mode of producing a plurality of terminal chlamydospores on a single conidiophore in the Hyphomycetes, and in the Coelomycetes apparently, that it must be taken into account in the future if conidium origin is to play any part at all in classification. (The annellations of Section III are comparable with the 'caps' formed in *Oedogonium* during cell formation (Fritsch (39))). The chlamydospores are nearly all dry.

Section IV.—The conidia are '*phialospores*' and are produced in basipetal succession from *phialides* which may or may not possess a very evident collarette. If the spores produced 'on the surface' of the ascospores of *Nectria coryli*, whilst still within the ascus, are the homologues of phialospores as suggested by Mr. Mason (82) then they may be called *radula phialospores*. The term *polyphialide* was proposed by Hughes (52) to include phialides which produce more than one open end from each of which a basipetal succession of phialospores is produced.

Langeron (76) included as phialides the annellophores of *Venturia inaequalis* [Sect. III], the conidiophores of *Erysiphe graminis* DC. [Sect. V], the sporogenous cells of *Beauveria bassiana* (Bals.) Vuill. [Sect. II], the sporogenous cells of '*Haplographium delicatum*' [Sect. IA] in addition to the true phialides of say *Stachylidium* and *Acrostalagmus* [*Verticillium*].

Mason (83) has pointed out that amongst fungi with phialides there is an 'obvious transition between genera characterized by slimy phialospores to other genera characterized by dry phialospores'.

Section V.—The conidia may be termed *meristem arthrospores* and they occur in true chains; their basipetal development, due to the meristematic growth

of the conidiophore, seems to me to necessitate a special term for them although they appear to be related to the arthospores dealt with in *Section VII.* Meristem arthrospores are usually dry.

Section VI.—The conidia may be called *porospores.* In *Helminthosporium velutinum* a solitary apical and lateral porospores in verticils are produced whilst in '*H. teres*' successive *terminus porospores* develop. Chains of porospores occur in *Diplococcium spicatum* and *Dendryphion* spp. Porospores are dry.

Section VII —The conidia have been called '*arthrospores*' and this seems to be a perfectly suitable term for conidia which arise from the fragmentation of conidiophores of determinate length. Arthrospores may be dry or slimy.

Section VIII.—The conidia are blown-out ends and are borne either singly at the apex or singly at the apex and laterally, generally in basipetal whorls. Mason (82) proposed the term 'radula thallospores' for the conidia of *Papularia* but I doubt whether this term can be used for Section VIII in its entirety. But the hall mark of this Section is the basal elongation of the conidiophores and these may be called *basauxic conidiophores.* The conidia are dry.

Because a taxonomic species is entitled to one and only one Latin binomial, some difficulty is experienced with the Fungi Imperfecti. Where a particular taxon has no recognized perfect state and is known to produce two or more imperfect states then any of the states is eligible to provide the generic name regardless of the relative position of the states in any scheme of classification. But which state should be chosen to supply the generic name for the taxon? Or is the particular association of different states to be the basis of a new generic name?

Mason (83) has drawn attention to a splendid example of a fungus described under seven binomials each generic name employed indicating the type of state under consideration. As Mason so rightly pointed out 'It is now, I think, generally agreed that seven binomials for one species are too many'.

It is interesting to observe that the generic name *Chalaropsis* Peyr. is based on a polymorphic species with two types of fructifications or states which would, separately, be classified in Sections IV (phialospores) and II (terminus spores) (see Mason (84)); the production of the two states is, I take it, obligatory for inclusion in *Chalaropsis.* The two types of conidium-bearing structures usually have a common stalk in *Chalaropsis thielavioides* Peyr., the type species, and also in *Ceratostomella radicicola* Bliss (10) (*Chalaropsis* state). The name '*Chalaropsis* pro parte', therefore, could be included in each of two Sections of the classification outlined above. *Thielaviopsis basicola* (Berk. & Br.) Ferr. (see Arnaud and Barthelet (2)) shows a similar association of distinct states also usually borne on a common stalk; the two states would be included, separately, in Sections IV (phialospores) and presumably II (chlamydospores). As Mason (84) has pointed out the two states of

Chalaropsis thielavioides Peyr. had already been described by McAlpine as '*Cylindrium intermixtum*' (phialospores) and '*Coniosporium radicicola*' (terminus spores). The former state could, I believe, be classified in *Chalara* but I know no generic name which would include comfortably the latter state. Is it advisable to base a generic name on the association of two states of one fungus? Now Mason (82) stated 'that the most urgent business of systematic mycology among the imperfect forms . . . must be to recognize whether a form-genus is founded on a phialospore form or is based on some other spore form . . .' But the form genera *Chalaropsis* and *Thielaviopsis* are each based on two different states or spore-forms although one state is common to both; I believe that such a practice is undesirable because the names are double form generic names relying on the presence of two distinct states for their precise application.

Not many 'species' of Fungi Imperfecti show such a constant association of two states on a common stalk; on the other hand most 'species' show a spasmodic occurrence of different states invariably on distinct stalks and furthermore many 'species' exhibit such different states only in pure culture on agar media.

If a fungus imperfectus shows itself to be polymorphic then it seems best to choose for the generic name of the taxon that state which is considered to be most frequent or constant in occurrence, most conspicuous, or most readily identifiable; but of course this is, for the most part, what has been done in the past. It would appear, therefore, that the choice of generic name for a polymorphic fungus imperfectus is entirely an arbitrary one. In such a polymorphic taxon, therefore, the generic name is the result of classifying one of the states or spore forms to the exclusion of all others (except in *Chalaropsis* for instance). But what of the states whose production is not implied by the generic name chosen? Mason advocated the use of differential names for classifying spore forms [states] and this seems to be the only way out with the Fungi Imperfecti. The subsidiary states may be referred to as *Hyalodendron* blastospores, *Cephalosporium* phialospores, etc., as the case may be, without the unnecessary new combinations. If no suitable qualifying generic name is available precisely to indicate the type of subsidiary state then this can be referred to by the use of spore terminology alone; but for this to work, of course, it is necessary to establish types of conidium development on a firm basis. The alternative is a multiplicity of names, that is, as many names for each species as any author considers there are of recognizable states.

Cooke's (21) concluding remarks in a note on 'Spores and Sporidia' are as follows: 'Subsidiary names are constantly being given to spores having a peculiar mode of generation or of development, and so long as these terms are understood and restricted to their original characteristics they are useful . . . . .'

In the scheme outlined above I have incorporated some old and some new ideas with old and new names for conidiophores and conidia. It is hoped that this comprises another step forward in the quest for a rational classification of those states currently classified as Hyphomycetes.

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DAOM 1056, on *Hordeum vulgare* leaves, Melfort, Sask., Canada, 18.viii.1931; 1749, on *Sambucus glauca*, near Northport, Wash., U.S., 24.viii.1929; 14161, isolated from seeds of *Brassica napa*, Ont., Canada, 1944; 14937, solated from seeds of *Cucumis sativa*, Pa., U.S., 1943; 14970, isolated from seeds of *Trifolium pratense*, Que., Canada, 1944; 14976, isolated from seeds of *Allium cepa*, Calif., U.S., 1944; 22593, isolation ex Forest Prod. Res. Lab., Culture collection no. 5-89; 28286(*b*), on *Fagus grandifolia*, Hermit Trail, near Pink Lake, Que., Canada, 9.viii.1952; 28732(*b*), isolated from *Pinus monticola*, Victoria, B.C., Canada, 1951; 28797, isolated from *Betula papyrifera*, Fredericton, N.B., Canada, 1952; 28997, on wood, Kingsmere, Que., Canada, 6.x.1952; 29102, isolated from Binocular reticule, Canal Zone; 29146, on wood, Burnet, Que., Canada, 1.x.1952; 29164, isolated from *Picea glauca*, Alta., Canada, 1951; 29291(*a*), on wood, Michigan Hollow, N.Y., U.S., 4.ix.1952; 29394(*a*), on wood, McLean, N.Y., U.S., 5.ix.1952; 29409, on wood, Ringwood, N.Y., U.S., 6.ix.1952; 29423(*a*), on wood, Coy Glen, N.Y., U.S., 4.ix.1952; 33739, isolated from *Betula lutea*, N.B., Canada, 1951; 33941, isolated from bark beetles, Black Sturgeon Field Sta., Thunder Bay district, Ont., Canada, 1952; 33997, isolated from larva of *Neodiprion sertifer*, Strathroy, Ont., Canada, 15.vii.1952; 34510, on *Carpinus caroliniana* var. *virginiana*, Chelsea, Que., Canada, 26.ix.1902; 35198, on *Juglans* sp., Ottawa, Canada, 11.xi.1952.

I.M.I. 349(*a*), on *Ligustrum ovalifolium*, Lambourne Hill, Perranzabuloe, West Cornwall, England, U.K., 16.xi.1944; 462, on *Fraxinus excelsior*, Mickleham, Surrey, England, U.K., 5.vi.1932; 1353, on *Crataegus oxyacantha*, Kingthorpe Woods, Yorks., England, x.1945; 1354, on *Fagus sylvatica*, Kingthorpe Woods, Yorks. England, x.1945; 1357, on wood, Kingthorpe Woods, Yorks., England, x.1945; 1359, on *Urtica* stems, Kingthorpe Woods, Yorks., England, x.1945; 1685, on *Solanum tuberosum*, England, xi.1945; 1694, 'Kings Cliffe', *Cladotrichum triseptatum* folder in Herb. R.B.G. Kew [no further data]; 4133, on *Urtica dioica*, Hampton Court, Middlesex, England, ii.1946; 4333, on *Urtica dioica*, near Aberystwyth, Wales, U.K., 25.iii.1946; 4493, on *Fagus sylvatica*, Boxhill, Surrey, England, 13.iv.1946; 5366, on wood, Norbury Park, England, 12.v.1946; 5505, on *Ulmus* sp. wood, Scarthingwell Park, Tadcaster, Yorks., England, 11.v.1946; 6054(*a*), on *Fagus sylvatica* wood, Tothill, Surrey, England, 7.vii.1946; 6072, on *Quercus* sp. wood, Ranmore, Surrey, England, 13.vii.1946; 6784, on *Quercus* wood, Mulgrave Woods, Yorks, England, 14.ix.1946; 6787, on *Tilia europea*, Forge Valley, Yorks, England, 16.ix.1949; 7040, on *Fagus sylvatica*, Arncliffe woods, Yorks, England, 17.ix.1946; 7393, isolated from Orange, Calcutta, India, 1939; 8977, on *Ranunculus* leaf, Simondsdyke Wood, England, 22.i.1946; 9070 (slide ex) *Conoplea tiliae* folder in Herb. Persoon in Herb. Lugd. Bat. No. 910, 263-286; 9882, on *Quercus* sp., Ranmore, Surrey, England, 6.i.1947; 14014, on *Fraxinus excelsior*, Howldale, Yorks, England, 13.iv.1947; 14486, on *Fraxinus excelsior*, Howldale, Yorks, England, 12.iv.1947; 15281,

on *Cladium mariscus*, Pool Marsh, Wheatfen Broad, Norfolk, England, 8.v.1947; 15528, on *Fagus sylvatica*, Ranmore, Surrey, England, 25.v.1947; 18435(*b*), on wood, Birmingham, England, ix.1947; 19039, on *Fraxinus excelsior*, Exeter, Devon, England, 14.ix.1947; 19219, on *Fagus sylvatica* cupules, near Masham, Yorks, England, 11.x.1947; 19654, on *Quercus ilex* twigs, Italy (D. Sacc., Fungi, Ven. Nov.); 20037(*d*), on *Betula*, Ranmore, Surrey, England, 14.xii.1947; 22419, on wood, Earls Court, London, England, 25.i.1948; 27623, on *Sorbus aucuparia*, Limb Valley, Yorks, England, 10.iv.1948; 31422, on *Ilex aquifolium*, near Masham, Yorks, England, 28.iv.1948; 33713, on *Fagus sylvatica*, Ranmore, Surrey, England, 23.i.1949; 34001(*c*), on *Brassica* sp., near Stoke Poges, Bucks, England, 23.i.1949; 40653(*g*) on *Sorbus aucuparia*, near Masham, Yorks, England, 15.iv.1950; 45947, isolated from soil, Sussex, England, xi.1950; 49478, on *Fagus sylvatica*, Ranmore, Surrey, England, ii.1952.

New Species, New Genera, New Combinations

Twenty-nine new combinations have been made throughout the text on pp. 582, 585 (two), 586, 587, 591, 594 (two), 603, 604, 605, 606, 609, 615, 616, 618, 619 (three), 622, 627, 628, 631, 634 (three), 636, 638, and 640, and six are proposed below.

A discussion, with fuller descriptions and further illustrations, of the new taxa described and reasons for many of the new combinations will be given in subsequent publications.

Section II: **Verticicladiella** gen. nov.

Fungi Imperfecti hyphomycetes.

Conidiophora sicut *Verticicladii* (typus *V. trifidum* Preuss) sed capitulo mucoso; ramulis primariis, secondariis, tertiisque plus minusve parallelis, adpressisque; cellulis sporogenis sub-parallelis.

Conidia continua, hyalina, ovata vel paulo curvata, laevia, acropleurogena in cellulis sporogenis in capitulum mucosum oriunda.

Species typica: **Verticicladiella abietina** (Peck) comb. nov.

≡ *Sporocybe abietina* Peck in N.Y. State Museum Rept. 31 : 45. 1879.

≡ *Periconia abietina* (Peck) Sacc. in Sylloge Fungorum, 4 : 273. 1886.

Section II: **Virgariella** gen. nov.

Fungi Imperfecti hyphomycetes, saprophytici.

Conidiophora longa, solitaria, simplicia, septata, crasso-tunicata, atro-brunnea.

Conidia sphaeroidea vel ovata, continua, atro-brunnea, laevia, sicca, crasso-tunicata, acropleurogena.

Species typica: **Virgariella globigera** (Sacc. & Ell.) comb. nov.
≡ *Virgaria globigera* Sacc. & Ellis apud Sacc. in Michelia, 2 : 578. 1882.

Species aliae: **Virgariella fusca** (Cooke) comb. nov.
≡ *Haplaria fusca* Cooke in Grevillea, 6 : 141. 1878.
≡ *Virgaria fusca* (Cooke) Sacc. in Sylloge Fungorum, 4 : 281. 1886.
= *Virgaria olivacea* Ell. & Everh. in Bull. Torrey Botan. Club, 10 : 97. 1883.

Virgariella atra sp. nov.

Coloniae atrae, effusae.

Mycelium immersum vel semi-immersum, ex hyphis ramosis, pallide-brunneis vel brunneis, septatis compositum.

Conidiophora solitaria, erecta, plus minusve rigida, recta, aliquando flexuosa, atro-brunnea, septata, crasso-tunicata, subcylindracea, usque ad 180μ longa, 3.5-5μ crassa, basi usque ad 6.5μ inflata. Crescentia conidiophori indefinita ut in finem cicatrices dispositi sunt in symplegmis intercalaribus.

Conidia subsphaeroidea vel ovata, continua, atro-brunnea, laevia, sicca, crasso-tunicata, acropleurogena, 13-13.5 × 9.7-12μ.

Habitat in ligno putrido *Fraxini excelsius*, Maltby, Yorkshire, Anglia, 9.iv.1948. I.M.I. 27613 (typus).

Section III: **Monosporella** gen. nov.

Fungi Imperfecti hyphomycetes saprophytici.

Conidiophora solitaria, simplicia, septata, crasso-tunicata, plus minusve subulata, brunnea, per proliferationes successivas cylindraceas elongascentia.

Conidia solitaria in primis in apice conidiophori et deinde successivarum proliferationum oriunda, sphaeroidea vel pyriformia, continua vel 2-septata, atro-brunnea vel brunnea, laevia, sicca.

Species typica: **Monosporella setosa** (Berk. & Curt.) comb. nov.
≡ *Monotospora setosa* Berk. & Curt. apud Berk. in Grevillea, 3 : 101. 1875.
≡ *Phragmocephala setosa* (Berk. & Curt.) Mason & Hughes in Naturalist, Lond. 1951 : 97. 1951.

Species aliae: **Monosporella sphaerocephala** (Berk. & Br.) comb. nov.
≡ *Monotospora sphaerocephala* Berk. & Br. in Ann. Mag. Nat. Hist. III, 3 : 361. 1859.
≡ *Halysium sphaerocephalum* (Berk. & Br.) Vuillemin in Bull. Soc. Sci. Nancy, III, 11 : 167. 1911.

A *Monosporella* conidial apparatus is also produced by *Farlowiella carmichaeliana* (Berk.) Sacc.

Section III: **Bactrodesmium masonii** sp. nov.

Sporodochia punctiformia, atra, dispersa, usque ad 170μ diam.

Conidiophora brevia, ramosa, septata, usque ad 37μ longa, hyalina vel subhyalina, basi 2.5-3μ, apicem versus usque ad 6μ crassa, per 1-3 proliferationes successivas cylindraceas elongascentia.

Conidia solitaria in primis in apice conidiophori et deinde successivarum proliferationum oriunda, ovata, 1-2 plerumque 2-septata, paulo constricta, crasso-tunicata, apice rotundata, basi plana cicatrice conspicuo praedita, pallide-brunnea, laevia, 18-26 × 8-10μ.

Habitat in cupulis emortuis *Fagi sylvatici* in terram; prope Masham, Yorkshire, Anglia, 11.x.1947, I.M.I. 19219(*y*) (typus); Boxhill, Surrey, Anglia, 22.xi.1947, I.M.I. 19652(*c*).

Section VI: **Dendryphiopsis** gen. nov.

Fungi Imperfecti hyphomycetes saprophytici.

Conidiophora: Stipes erectus, septatus; ramuli laterales primarii, secondarii, ternarii, quandoque quaternii, solitarii vel plerumque bini oriundi, plus minusve in formam dichasii. Stipes, ramulique poro singulo apicali praedita.

Conidia singula in ramo, in apicibus stipitis ramulorumque oriunda, subcylindracea, utrinque rotundata, crasso-tunicata, 2-6-septata, laevia, fortiter colorata, facile secedentia, basa poro praedita.

Species typica: **Dendryphiopsis atra** (Corda) comb. nov.
≡ *Dendryphion atrum* Corda in Icones Fungorum, 4 : 33. 1840 (sub '*Dendryphium*').
= *Dendryphion ellisii* Cooke in Grevillea, 7 : 7. 1878 (sub '*Dendryphium*').

Identical with *D. atra* or only critically distinct from it are the following:

Helminthosporium nanum Nees in Das System der Pilze und Schwamme. 1817.

Helminthosporium obtusissimum Berk. & Curt. apud Berk. in Grevillea, 3 : 103. 1875.

Dendryphion crustaceum Ell. & Everh. in Webber Rept., Nebr. Bd. Agr. 1889 : 85. 1890 (sub '*Dendryphium*').

Dendryphion pachysporum Ell. & Everh. in Proc. Acad. Phil. 1891 : 92. 1891 (sub '*Dendryphium*').

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NOTE: Since this article went to press *Streptothrix* conidiophores have been obtained from pure cultures of *Urnula craterium* (Schw.) H. (See p. 606).

A NEW NATURAL HYBRID *CYPRIPEDIUM* FROM ONTARIO[1]

By Leslie A. Garay[2]

Abstract

It is the intention of the author in the following paragraphs to discuss and describe a natural hybrid of the genus *Cypripedium*, from Ontario, Canada, and to call it *Cypripedium Landonii* in honor of its discoverer. This new hybrid is considered to be a cross between *Cypripedium Calceolus* L. var. *parviflorum* Fern. and × *Cypripedium Favillianum* Curtis. This conclusion is based on the variability of the staminode, of which some forty were examined in the field and in the laboratory. The included plate illustrates that these staminodes approach the shape of their parents.

Introduction

In 1949 a rather peculiar looking herbarium specimen came to the writer's attention. This specimen upon initial inspection bore a marked resemblance to the well-known *Cypripedium Calceolus* var. *pubescens* Correll. On more extended examination, however, there came to light so many differing diagnostic features that it became evident that further investigation was required. The herbaria of the University of Toronto and of McMaster University, both of which are richly supplied with collections of Southern Ontario specimens, netted a good series of this questionable species. It was noted that all these collections came from the same area and were collected by Mr. Monroe Landon.

Further, in 1951, during a visit to Turkey Point, several clumps of this species were found in association with *C. Calceolus* var. *parviflorum* Fern.,—var. *pubescens* Correll, and *C. candidum* Muhl. It should be mentioned also, that we found here × *C. Favillianum* Curtis (1) and × *C. Andrewsii* Fuller (2), for both of which this seems to be the first report for Ontario. The author immediately suspected that our plant was also a natural hybrid. Many specimens were examined in the field. Some forty staminodes of these were collected and preserved in FAA*, and upon re-examination in the laboratory (consideration of their characteristics), a new natural hybrid is accordingly recognized.

Description and Discussion of the Species

Cypripedium Landonii Garay, hybr. nov. nat.

Herba caespitosa; radicibus fasciculatis, satis longis, fibrosis, glabris; caulibus elongatis, teretibus, pubescentibus, primum ad solum vergens repentis, deinde ascendentibus, flexuosis, laxe foliatis, 1-2-floris; pars repente 4-vaginato, vaginis obliquis, acutis, leviter sulcatis, ad 10 cm. longis; pars ascendente laxe 4-foliato; foliis lanceolatis, illis *C. candidi* simillimis sed

[1] *Manuscript received June 3, 1953.*
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* *Formalin-acetic-alcohol.*

valde divergentibus, breviter caulem amplectentem petiolatis, parum conduplicatis, acuminatis, margine undulatis, utrinque pubescentibus, ad 20 cm. longis, 5 cm. latis; bracteis foliaceis, lanceolato-acuminatis, sensim undulatis, floribus semper superantibus; floribus illis *C. Calceoli* var. *parviflori* simillimis et fere aequimagnis; sepalo postico ovato-lanceolato, acuminato, sensim concavo, apice leviter undulato-torquato, ad 4 cm. longo, 1.5 cm. lato; lateralibus in synsepalo coalitis, bifidis, dorsale fere aequimagnis latisque; petalis linearibus, acuminatis, planis seu sensim spiraliter-torquatis, divergentibus, ad 4 cm. longis, 0.5 cm. latis; sepalis petalisque basin versus distincte pubescentibus; labello calceolari, inflato, ovoideo, lateraliter leviter compresso, obtuso, usque ad 2.5 cm. longo; orificio subrotundo, ca. 1 cm. diam.; columna generis; staminodio oblique ovato, obtusa, distincte unguiculato illis *C. Favilliani* simillimo sed valde variabile; ovariis longe pedicellatis, cylindraceis, pubescentibus.

Caespitose plants with fasciculate, fibrous roots; the stem first decumbent then ascending, elongate, slightly flexuose, terete, and pubescent, terminating in a one- or two-flowered raceme; the decumbent portion is covered with four sheaths which are oblique, acute, somewhat sulcate, and up to 10 cm. long; the ascending part loosely three–four-foliate; the leaves are lanceolate, resembling those of *C. candidum* in shape but strongly divergent, somewhat conduplicate, acuminate, becoming narrower towards the base, imbricating each other and enclosing the stem, up to 20 cm. long, 5 cm. broad; the foliaceous bracts are lanceolate, acuminate, somewhat undulate, and always overtopping the flowers; the flowers are like those of *C. Calceolus* var. *parviflorum* and are about the same size; the dorsal sepal is ovate-lanceolate in outline, slightly concave with an acuminate, somewhat undulate or sometimes twisted tip, 4 cm. long and 1.5 cm. broad; the lateral sepals are united into a bifid synsepal, which is similar in shape and size to the dorsal one; the petals are linear, acuminate, sometimes slightly twisted toward the tip, 4 cm. long, 0.5 cm. broad; both sepals and petals are distinctly pubescent toward their bases; the lip is pouch-shaped, ovoid, laterally slightly compressed, obtuse, with a subrotund opening of 1 cm. in diameter, up to 2.5 cm. long; the column is generic; the staminode is variable, distinctly unguiculate, ovate, obtuse with an asymmetrical base; the ovary is long-pedicelled, cylindric, and pubescent.

Specimens Examined:

CANADA: **Province of Ontario;** Turkey Point, Lake Erie, Norfolk County, at edge of cedar woods along base of shore cliff. – Coll.: *J. H. Soper, K. L. Hull, and L. A. Garay s.n.* (*Type !*) – Type in the herbarium of the Department of Botany, University of Toronto (TRT) No. 71.562. Part of the type collection is in the author's herbarium No. 1.181; – also the same locality *M. Landon* s.n. ! (TRT, McM).

Cypripedium Landonii is considered by the writer to be a natural hybrid between *C. Calceolus* var. *parviflorum* and × *C. Favillianum.* The arrange-

ment and shape of the leaves show definitely the character of both *C. candidum* and the previously described hybrid *C. Favillianum* (Fig. 1). However, the color of the flower and the size of the entire plant resemble *C. Calceolus* var. *parviflorum*, whose characters seem to dominate. The staminode, as the attached plate shows (Figs. 2-7), is greatly variable. The six forms here represented were carefully selected to illustrate the closest approach to the parents. All the staminodes have a long claw as in the typical *C. candidum*. Fig. 2 represents the closest approach to *C. Calceolus* var. *parviflorum*, as the shape appears to be broadly oblong with a symmetrical base, while in the typical it is cuneate-oblong or triangular. Figs. 3-4 are similar to × *C. Favillianum*, i.e. the shape is broadly oblong or cordate with an asymmetrical base. Figs. 5-7 resemble *C. candidum* in the narrow ovate or oblong shape, but have an asymmetrical base. Since the shape of the staminode is the main guide for segregating the species in the whole subtribe *Cypripedilinae*, the variability in its shape should support the recognition of this new hybrid. It should be mentioned that Mr. Landon has observed these plants over a period of 20 years, and found a large series of intermediate forms of the earlier described hybrids, but this one seemed to him to have constant characters. The writer has had the opportunity to study the types of *C. Andrewsii* and *C. Favillianum* and a large series of the intermediate forms of these two hybrids, thus his study excludes the possibility that the species here described is one of these.

It would seem to be unnecessary to enumerate the examined specimens from the above mentioned herbaria, since with the exception of the type, all were collected by Mr. Landon at the same spot over a period of years.

It is a pleasure to name this plant in honor of Mr. Monroe Landon, an outstanding naturalist of Simcoe.

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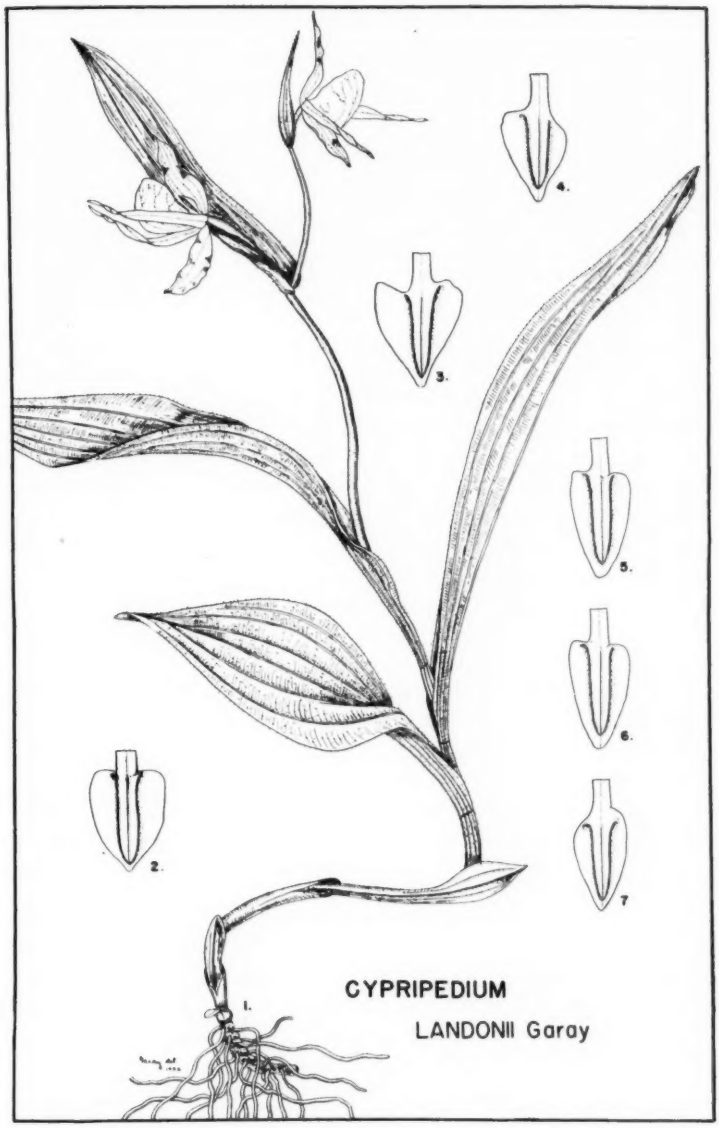

FIG. 1. Plant about one half of the natural size. FIGS. 2-7. Various staminodes approaching the shape of the parents, ×2. FIG. 2. Similar to *C. Calceolus* var. *parviflorum* Fern. FIGS. 3-4. Close to × *C. Favillianum* Curtis. FIGS. 5-7. Resembling *C. candidum* Muhl.

NOTES ON BOREAL USTILAGINALES[1]

By D. B. O. Savile[2]

Abstract

A number of new records of smut fungi, largely from northern Canada, are listed. *Thecaphora apicis* (on *Carex pyrenaica*), *Ustilago cilinodis* (on *Polygonum cilinode*), and *U. anomala* Kunze var. *tovarae* (on *Polygonum virginianum*) are described as new. *Ustilago punctata* Clint. is shown to be synonymous with *U. bosniaca* G. Beck. *Ustilago polygoni-punctati* nom. nov. is proposed in place of the invalid name *U. microspora* (Speg.) Liro. *Ustilago anomala* Kunze var. *cordai* (Liro) Savile and *U. violacea* (Pers.) Roussel var. *stellariae* (Sow.) Savile are proposed as new combinations.

Many of the following notes stem from collections made by members of the Division of Botany and Plant Pathology while serving as botanists with field parties of the Northern Insect Survey in Northern Canada or Alaska, under the sponsorship of the Defence Research Board, Department of National Defence. Several notable records from southern Canada have also been included. In a few instances study of Canadian specimens has involved the revision of smut or host determinations for specimens from the United States.

Some of these records are given by Fischer (3), but others came to light only after the *Manual* had gone to press. Only such synonymy is given below as is needed for clarity, since, in most instances, Fischer gives the synonymy in detail.

Doassansia epilobii Farl. (Botan. Gaz. 8 : 277. 1883)

This extremely inconspicuous species was collected on *Epilobium palustre* L. at Great Whale River, Que., in July and August 1949 (Savile 493, 601). It was noticed only because small plants infected by *Pucciniastrum* were being pulled up, and the minute sori were just visible on the lower leaves. It seems to be scarce as well as inconspicuous, for the writer has failed to find it since in apparently favorable habitats.

Doassansia martianoffiana (Thüm.) Schröt. (Krypt. Fl. Schles. 3 : 287. 1887)

A light infection occurred on *Potamogeton epihydrus* Raf. var. *nuttallii* (Cham. & Schlecht.) Fern., between Fairbanks and College, Alaska, in July 1951 (W. J. Cody 6080). The nearest reports are from Washington and Manitoba. A specimen from near Ottawa, Ont., on *P. americanus* R. & S., Aug. 1948 (DAOM 20593) was inadvertently omitted when Canadian records were sent to Dr. Fischer for the *Manual*.

[1] *Manuscript received June 1, 1953.*

Contribution No. 1281 from the Division of Botany and Plant Pathology, Science Service, Department of Agriculture, Ottawa, Canada.

[2] *Mycologist.*

ENTYLOMA COMPOSITARUM Farl. (Botan. Gaz. 8 : 275. 1883)

Found in phanerogamic specimens of *Erigeron humilis* Graham (syn. *E. unalaschkensis* (DC.) Vierh.), Coral Harbour, Southampton I., Dist. of Keewatin (W. J. Cody 1566), and *Senecio cymbalarioides* Nutt., Yellowknife R., Dist. of Mackenzie (W. J. Cody and B. J. McCanse 2178). In these two northern specimens there is no sign of conidia or conidiophores, which are almost universally present, further south, in this species. The situation is apparently analagous to that in certain short-cycled *Puccinia* spp. that are leptosporic in the south but not in the north. A conidial state is of minor value in the short northern summer, but the mechanism by which it is suppressed is obscure.

ENTYLOMA LINARIAE Schröt. (*In* Cohn Beitr. Biol. Pflanz. 2 : 371. 1877)

A trace was found on *Veronica americana* (Raf.) Schwein., Rupert House, James Bay, Que. (F. G. Spafford 78). A substantial northward range extension.

THECAPHORA ATERRIMA Tul. (Ann. sci. nat., Botan., III, 7 : 110. 1847)

This well-named species, with spore balls extremely opaque even after boiling in lactophenol, was until recently unreported in Canada. It was found in a collection of *Carex filifolia* Nutt. (*s. l.*) from Carcross, Yukon, 21 July 1949 (J. M. Gillett 3916). Later a trace was found, mixed with *Cintractia externa*, on the same host from Punnichy, Sask., 21 Aug. 1938 (C. L. and R. C. Russell). Spore balls 18.0–56.0 × 14.5–47.0μ. Spores 10.0–15.5μ long, outer wall chestnut to black, with irregular warts to 0.8μ high, to 1.3μ wide; (1–)2–?40 spores per ball (about 20 in moderately large balls, but opacity prohibits counts in the largest). In addition to the hosts given by Fischer (3) it attacks various *Carex* spp. in Europe.

Thecaphora apicis Savile sp. nov.

Ovarium degenerat in soro quis perigynium fragat et *Cintractiam* simulat; sorus insuper sphaericus, pulverulans, atro-brunneus; sporae conglobatae in mole spissa ex (1–)2–12 sporis, cellulis sterilibus deentibus. Moles (10.5–) 13.0–22.5 × 9.0–19.0μ. Sporae 6.0–11.0 × 6.0–9.0μ; paries 0.5–0.8μ crass., luteo-brunneus, laevis vel subrugosus in latere exteriori, complanatus in lateribus interioribus.

In ovaries of *Carex pyrenaica* Wahl., Apex Mountain, 15 miles northwest of Keremeos, B.C., 6 Sept. 1951 (H. A. Senn, C. Frankton, and J. M. Gillett 5783) TYPE; DAOM 34034 in Mycological Herbarium, Div. of Botany and Plant Pathology, Dept. of Agriculture, Ottawa; a fragment also in Dept. of Plant Pathology, State College of Washington, Pullman, Wash.

This smut is quite distinct from *Thecaphora aterrima*, and appreciably different from *T. rhynchosporae*, which has larger spore balls and slightly larger spores.

TOLYPOSPORIUM BULLATUM (Schröt.) Schröt. (Krypt. Fl. Schles. 3 : 276. 1887)

The recent finding of this species near Bourget, Russell Co., Ont. (W. G. Dore and W. J. Cody 14048) on *Echinochloa walteri* (Pursh) Heller, led to a re-examination of specimens in the herbarium. Dr. Dore has checked the hosts, and Canadian specimens include one from Nova Scotia on *E. crusgalli* (L.) Beauv. (received as such), and two from Toronto, Ont., on *E. pungens* (Poir.) Rydb. var. *microstachya* (Wieg.) Fern. & Grisc., received as *E. crusgalli* and unfortunately reported to Dr. Fischer as such. We also have part of H. S. Jackson's collection from Indiana, supposedly on *E. walteri*, but the host appears to be *E. pungens* var. *wiegandii* Fassett, although, lacking leaves, positive determination is not possible.

Clinton (1) described the spores of *Tolyposporium bullatum* as being held together by interlocking ridges, and Fischer (3) uses much the same description in his generic diagnosis. Such a conformation seemed dynamically so improbable in a densely compacted spore ball that the morphology was re-examined. Careful examination shows that the ridges occur sporadically and and consist of broken spore walls, and that the spore surface is covered by contiguous polygons. If spore balls are well cleared and examined before crushing, it will be seen that there is almost no free space between the spores, certainly not enough for high ridges. The polygonal flats on the spore surfaces are clearly the result of mutual compression. It should be explained that the smaller balls are spheroidal, resembling, if the analogy may be allowed, little rabbit pellets; whereas the largest, running up to 250μ long, consist of several small balls fused together, like sheep droppings. Avoiding these very large balls, which seriously obscure vision, and the very small ones, in which the majority of spores are at or near the surface, a mount was made from the larger spheroidal balls. After the spore balls were boiled in lactophenol, it could be seen that most of the inner spores departed little from spherical form. The spore balls were then teased open as gently as possible, with the result that very few spores bore the ridges that are actually fragments of adjoining spores. The spores are too small, and too difficult to manipulate, for an exact analysis to be made; but some appear to approach the tetrakaidekahedron, the perfect space-filling figure, as closely as any biological example cited by Thompson (9). Thus a perfect square can occasionally be seen to be bounded by four nearly perfect hexagons. The polygon boundaries do not stand up as wings, except when two spores are so firmly joined that one breaks before they separate. There is, however, the slight internal thickening along them that typically occurs in the angle of any wall.

UROCYSTIS AGROPYRI (Preuss) Schröt. (Abh. Schles. Ges. Abth. Nat. Med. 1869–1872 : 7. 1869)

(*Tubercinia triseti* Cif., Ann. Mycol. 29 : 14. 1931)

(*Tubercinia elymi* Cif., Ann. Mycol. 29 : 17. 1931)

The records discussed below have been listed by Fischer (3), but the details are given here because they illustrate the difficulty of maintaining the many

recorded segregates of this complex as species. Collections were made on *Elymus mollis* Trin. (*E. arenarius* L. var. *villosus* E. Meyer) at Great Whale River, Que. (Savile 551) and Chesterfield Inlet, Dist. of Keewatin (Savile and C. T. Watts 1071, Savile 1363). The first two collections cited conform closely to the usual concept of the species, having 1–3(–4) and 1–2(–3) spores per ball respectively and spore balls *ca.* 19–32 × 16–24μ; but in Savile 1363 the spore balls are 22–57 × 17–34μ with 1–6(–7) spores per ball. In all collections the sterile envelope was nearly complete on most spores. A smut was also collected at Chesterfield Inlet on *Trisetum spicatum* (L.) Richt. var. *maidenii* (Gandoger) Fern. (Savile and C. T. Watts 1540), with spore balls 21–54 × 17–33μ and having 1–7(–8) spores and usually a more or less complete sterile envelope; i.e., scarcely distinguishable from Savile 1363. This specimen agrees closely with *Tubercinia triseti* Ciferri as described from Finland by Liro (7); but it must be noted that in Ciferri's original description, based on material from Norway, the balls are stated to contain one to three, typically two, spores. In all these specimens, and many others, the variations in the individual spores and sterile cells are generally no greater between than within hosts. It accordingly seems impossible, when a long series of specimens is considered, to disagree with the wide species concept of Fischer (2, 3). See Fischer for detailed synonymy.

UROCYSTIS ANEMONES (Pers.) Wint. (Rabenhorst. Krypt.-Fl. 1 : 123. 1881)

Recent northern collections have been made on *Ranunculus nivalis* L., Keno Hill, near Mayo, Yukon (J. M. Gillett *et al.* 4334); on *Anemone parviflora* Michx., Mt. Marathon, Kenai Peninsula, Alaska (J. A. Calder 6356); on *A. quinquefolia* L., Moose Factory, James Bay, Ont. (Savile 125). The Moose Factory specimen agrees closely with many other eastern collections, but the other two have fewer sterile cells per spore ball, and the sterile cells contrast relatively little with the spores. The agreement between these two specimens is very close. They might well be assigned to a distinct species, but the writer prefers to await a better series from intervening areas, because of a possible cline, before making a decision.

UROCYSTIS SOROSPORIOIDES Körn. (Fuckel, Symbolae Mycol. Nachtr. 3 : 10. 1875)

A single sorus was found on a stem of *Anemone narcissiflora* L. ssp. *interior* Hultén, at Mile 12, Paxton-Cantwell Highway, Alaska (T. J. M. Webster 216A). Already reported from Alaska on *A. narcissiflora* by Zundel (10) and Fischer (3).

USTILAGO BULLATA Berk. (Hooker, Fl. New Zealand, 2 : 196. 1855)

This species heavily infected *Hordeum jubatum* L. at Dawson, Yukon, in July 1949 (J. A. Calder and L. G. Billard 3878).

USTILAGO CALAMAGROSTIDIS (Fckl.) Clint. (J. Mycol. 8 : 138. 1902)
(*Tilletia calamagrostis* Fckl., Symbolae Mycol. 40. 1869)

This stripe smut was abundant in two colonies of *Calamagrostis canadensis* (Michx.) Nutt. var. *robusta* Vasey at Great Whale River, Que., in 1949 (Savile 550, 610). Included by Fischer (3) with *Ustilago striiformis* (Westend.) Niessl; but in these collections the spores are substantially larger (11.0–18.5 × 8.0–14.0μ) than those of typical *U. striiformis* and are shallowly verrucose, with rounded warts 0.2–0.3μ high, rather than echinulate.

USTILAGO RESIDUA Clint. (J. Mycol. 8 : 133. 1902)

Several infected plants were found in a small colony of *Danthonia intermedia* Vasey, at *ca.* 60° 37′ N. : 149° 33′ W., Kenai Peninsula, Alaska, 18 Aug. 1951 (J. A. Calder 6814). This record constitutes a northwestward range extension for the smut of about 1500 miles. It is particularly notable because *Danthonia* is extremely scarce in Alaska.

There is an interesting and seemingly natural group of purple-spored species of *Ustilago*, occurring chiefly on centrospermous plants (Polygonaceae, Portulacaceae, and Caryophyllaceae), but with single species also known on *Gayophytum* and *Pinguicula*. Recent collections have necessitated consideration of some of the species attacking Polygonaceae and Caryophyllaceae.

USTILAGO BISTORTARUM (DC.). Körn. (Hedw. 16 : 38. 1877)
(*Ustilago bistortarum* (DC.) Körn. var. *inflorescentiae* Trel., Harriman Alaska Exped. Crypt. Botan. 35. 1904)
(*Ustilago inflorescentiae* (Trel.) Maire, Oesterr. Botan. Z. 57 : 273. 1907)
(*Sphacelotheca hydropiperis* (Schum.) de Bary var. *borealis* Clint., Proc. Bost. Soc. Nat. Hist. 31 : 395. 1904)
(*Sphacelotheca borealis* (Clint.) Schellenb., Ann. Mycol. 5 : 386. 1907)
(*Sphacelotheca polygoni-vivipari* Schellenb., Ann. Mycol. 5 : 388. 1907)
(*Ustilago candollei* Tul., Ann. sci. nat., Botan., III, 7 : 93. 1847)
(*Ustilago marginalis* (DC.) Lév., in D'Orb. Dict. Univ. Hist. Nat. 12 : 778. 1848)
(*Ustilago pustulata* (DC.) Wint., Hedw. 18 : 109. 1880)
(*Ustilago ustilaginea* (DC.) Liro, Ann. Acad. Sci. Fennicae Ser. A, 17 : 7. 1924)

The above is a partial list of synonyms for what the writer is convinced is a single fungus causing localized infection of *Polygonum* spp. sect. *Bistorta*. The writer fully agrees with Hirschhorn (4) and Linder (5) that the spores of the leaf and floret infections are indistinguishable. The sori may occur along the leaf margin, randomly on the lamina, or in the florets. These distinctions have been used to define species, but it is doubtful whether they have even physiological significance. In some regions or seasons leaf infection may predominate, in other areas or seasons the florets are attacked most heavily. Floret infection is very common in the arctic, and is the phase usually found in

the examination of phanerogamic specimens, but a careful search of colonies of *P. viviparum* will often yield sori on the leaves also. At Chesterfield Inlet the type of infection seemed to vary with small differences in topography and exposure, even within a single colony. No doubt the microclimate affects the likelihood of infection in a particular organ. The degree of development of leaf or floret at the time of spore germination must also profoundly affect their susceptibility and so determine the infection pattern.

The over-all range of spore size in Canadian specimens seen on *Polygonum viviparum* is 7.6–18.0 × 6.3–14.5(–16.0)μ, but the ranges of individual specimens are usually substantially narrower. Specimens seen include: on *P. bistorta* L. ssp. *plumosum* (Small) Hultén; near Dawson, Yukon (J. A. Calder and L. G. Billard 3833). On *P. viviparum* L.; Mould Bay, 76° 19′ N.: 199° 34′ W., Prince Patrick I. (P. F. Bruggeman 458); 82° 32′ N.: 62° 30′ W. Ellesmere I. (P. F. Bruggeman 207); Spence Bay, 69° 30′ N.: 93° 28′ W. (J. G. Chillcott 65); Chesterfield Inlet, 63° 21′ N.: 90° 42′ W., (Savile and C. T. Watts 1081, 1112, 1146, 1231, 1232). Specimens on the latter host from Colorado and Sweden fall in the same size range. All specimens agree in having spore walls finely verrucose with warts about 0.2–0.3μ high, 0.2–0.4μ wide, and 0.5–1.2μ spacing between centers. It will be noted that this species has several times been assigned to the genus *Sphacelotheca*. The mycelial membrane of the sorus is not strongly developed in any of the specimens cited and seems to be an ephemeral and perhaps even an inconstant character. In *Sphacelotheca hydropiperis* on *P. hydropiper* (the type of the genus) the membrane appears to be somewhat more constant; but whether the genus should be maintained on such a character is debatable. The spores of the fungus on *P. hydropiper* cannot be distinguished with any certainty from those from *P. viviparum*, although the warts are possibly slightly shallower. Apart from the character of the sorus membrane the fungi are virtually identical and certainly could not be given more than varietal distinction. It is not improbable that an ontogenetic study of the sori will eventually indicate that the whole complex should be called *Ustilago hydropiperis* (Schum.) Schröt., perhaps with several physiologic forms and two or more varieties. The same problem of intergradation between *Ustilago* and *Sphacelotheca* is indicated in the next species. As Schellenberg (8, p. 61) remarked, other species of *Sphacelotheca* resemble individual species of *Ustilago*. At best the genus appears to be a polyphyletic outgrowth of *Ustilago*.

USTILAGO BOSNIACA G. Beck (Sched. ad Krypt. Exs. Cent. I. Ann. Nat. Hofmus. Wien, 9 : 121. 1894)

(*Ustilago punctata* Clint., North Am. Flora, 7 : 23. 1906)

(?*Sphacelotheca alpina* Schellenb., Ann. Mycol. 5 : 393. 1907)

The spores of the type collection of *Ustilago punctata*, on *Polygonum newberryi* Small from Mt. Adams, Wash.; of a specimen on *P. phytolaccaefolium* Meisn. (*P. alpinum* auct.) from Oregon Caves, Ore.; and of the type of *U. bosniaca*, on *P. alpinum* All., from Mt. Matorac, Bosnia (Yugoslavia) (Krypt.

Exs. Mus. Palat. Vindobon. 8), are all identical: 10.5–19.0(–20.5) × 9.5–15.5(–17.0)μ; wall deep brownish purple with cylindrical warts 0.3–0.6 (–0.8)μ high, 0.2–0.4μ wide, 0.4–1.2(–1.5)μ spacing between centers. Fischer (*in litt.*) sees no justification for placing *U. punctata*, of the type of which the writer has seen only a spore mount, in *Sphacelotheca*. The writer can see no justification for such a course in the other two specimens cited. Schellenberg (8, p. 72), however, admits that his *S. alpina* may be identical with *U. bosniaca* on the same host. Thus the problem of generic disposition discussed under the last species is here repeated. Clinton described the spores of his fungus as punctate, but they are actually verrucose, as Fischer (3) has already indicated. The three hosts cited, and *P. davisiae* Brew. cited by Fischer, are all in sect. *Aconogonum*; but *P. punctatum*, also cited by Fischer, is in sect. *Persicaria*, which usually takes *Sphacelotheca hydropiperis* or reticulate-spored species of *Ustilago*.

USTILAGO ANOMALA Kunze (F. Sel. Exs. 23. 1875) var. ANOMALA

This and closely related smuts on various species of *Polygonum* were split by Liro (6) into several species on the basis of demonstrated or apparent host specialization; but most of his taxa show extremely little morphological distinction and it is doubtful whether any merit more than varietal rank. *Ustilago anomala* was described on *P. dumetorum* L. The following description is based on the type collection and two other European collections on the same host: Spores 10.0–13.5 × 9.3–11.5μ. Wall with thin, light brownish purple outer layer, and with or without (in any collection) a thicker, subhyaline inner layer; conspicuously reticulate with meshes 0.4–1.2μ high, 1.2–2.7(–3.2)μ diam.

Not all Liro's entities have been seen, but from a study of collections on *Polygonum convolvulus* L., from Saskatchewan, Nova Scotia, and Moravia, the writer agrees with the disposition of this smut as *Ustilago anomala* var. *carnea* (Liro) Hirschhorn (4). The spores are 9.5–13.5 × 9.0–12.5μ; wall light yellowish mauve, with meshes 0.6–1.5μ high, 1.3–2.8μ diam. The only distinctions from the typical variety are the slightly paler walls and higher meshes.

The smut on *Polygonum hydropiper* L. is also just distinguishable and the following recombination accordingly seems to be merited:

USTILAGO ANOMALA Kunze var. **cordai** (Liro) Savile comb. nov.
(*Ustilago cordai* Liro, Ann. Acad. Sci. Fennicae Ser. A, 17 : 12. 1924)

This smut has slightly larger spores than var. *anomala* and the meshes are appreciably higher than in that variety and slightly higher than in var. *carnea*. Four collections from Ontario, Sweden, and Bohemia yield: Spores 9.5–14.5(–15.5) × 9.0–13.0μ; wall light to dark brownish purple, with meshes (0.6–)0.8–1.7μ high, (1.0–)1.4–3.0μ diam. Specimens on *P. hydropiper* have been assigned by Clinton (1), Zundel (10), and Fischer (3) to *U. utriculosa*; but their affinities are clearly with *U. anomala*.

A single specimen on *Polygonum virginianum* L. (*Tovara virginiana* (L.) Raf.) belongs in the present complex but is clearly a distinct variety. The following name is proposed:

USTILAGO ANOMALA Kunze var. **tovarae** Savile var. nov.

Differt sporis majoribus, 11.0–14.5(–17.0) × 10.3–13.5(–15.5)μ, scutulis altioribus, 1.0–1.7μ alt.

In ovaries of *Polygonum virginianum* L., Berthierville, Que., (DAOM 18882) leg. R. Pomerleau (TYPE).

A smut with much smaller spores than those of *U. anomala* was collected on *Polygonum punctatum* Ell. var. *majus* (Meisn.) Fassett, near Erinsville, Lennox & Addington Co., Ont., by G. Mulligan and W. G. Dore (DAOM 26772), and *P. punctatum* var. ?, Digby Co., N.S., by E. C. Smith *et al.* 7101. The spores are 7.0–11.5 × 6.5–10.0μ; the meshes on the spore wall are 0.5–1.4μ high, 0.8–2.3μ diam. (measured at the base as is necessary for uniformity where the meshes are large in relation to the spore). This is presumably the smut that Liro called *U. microspora*, and that Spegazzini first reported on *Polygonum acre* HBK. The latter plant is *P. punctatum* Ell. var. *punctatum*. Unfortunately the name *U. microspora* is preoccupied; therefore is is proposed to call this species:

Ustilago polygoni-punctati Savile nom. nov.

(*Ustilago microspora* (Speg.) Liro, Ann. Acad. Sci. Fennicae Ser. A, 17 : 234. 1924. Not *U. microspora* Schröt. & Henn., Hedw. 35 : 215. 1896)

(*Ustilago utriculosa* (Nees) Unger var. *microspora* Speg., Myc. Argent. Ser. 2 : 58. 1902).

There are several records in the literature of *U. utriculosa* on *P. punctatum*, but no other specimens have been seen.

A well-known smut on *Polygonum cilinode* Michx. has long passed as *Ustilago anomala*. It proves consistently to have substantially larger spores than that species and is best regarded as a distinct species. It is accordingly named:

Ustilago cilinodis Savile sp. nov.

Sporae 10.0–17.0 × 9.3–15.5μ; paries saturate brunneo-purpureus, scutulis (0.5–)0.8–1.7μ alt., 1.4–3.0μ diam. (vel usque ad 3.3μ long.).

In ovaries of *Polygonum cilinode* Michx., Liberty, N.Y. (Seymour & Earle Econ. Fungi 364, TYPE, in Division of Botany and Plant Pathology, Dept. of Agriculture, Ottawa). Abundant in western Quebec and Ontario, extending north to Fort Hope, Ont., 51° 34′ N.: 87° 59′ W. (A. Dutilly, E. Lepage, and M. Duman 30,617*a*).

USTILAGO UTRICULOSA (Nees) Unger (Einfl. d. Bod. 211. 1836)

(*Ustilago reticulata* Liro, Ann. Acad. Sci. Fennicae Ser. A, 17 : 20. 1924)

The name *Ustilago utriculosa* was abandoned by Liro presumably because Nees' fungus was not clearly typified. However, when Kunze, the first

critical student of the complex, segregated *U. anomala* in Kunze F. Sel. Exs. 23, it is significant that he issued as No. 22 in the same set *Ustilago utriculosa* on *Polygonum lapathifolium* L. This is the fungus that has since been recognized as *U. utriculosa* by most students of these smuts, and it seems quite unnecessary to drop a widely used and reasonably unambiguous name. The name for the principal host requires some clarification. The plants that for long passed as *P. lapathifolium* actually consist of two quite distinct species, *P. lapathifolium* L. and *P. scabrum* Moench (syn. *P. tomentosum* Schrank). After Dr. C. Frankton warned the writer of this situation a check was made of all available specimens. Not all hosts can be definitely identified, but the majority are certainly *P. scabrum* and the remainder are probably this species. Unfortunately enlightenment did not come until Fischer's *Manual* was coming off the press. Consequently most Canadian records for Alta., Ont., Que., N.B., N.S., and P.E.I., at least, are referable to *P. scabrum*. Kunze F. Sel. Exs. 22 is also apparently on *P. scabrum*, as are specimens from elsewhere in Germany and from Sweden. One collection from Denmark may be on *P. lapathifolium* or *P. nodosum*. There is thus some doubt whether *P. lapathifolium* is a host, although there is no reason why it should not be. All specimens examined on the related *P. pensylvanicum* L. are indistinguishable from those on *P. scabrum*. The meshes on the spores of this smut are so large in relation to the spores that the opposite sides diverge at a substantial angle. For uniformity the diameters of the meshes should accordingly be taken always at the same level. In the following description the diameters are for measurements at the base; that for a large mesh may be fully one micron more at the top. Spores 9.5–14.5(–15.5) × 9.0–13.0μ. Wall deep brownish purple, with meshes 0.8–2.0μ high, 1.5–4.5μ wide, or to 5.0(–6.0)μ long.

This smut, on *P. scabrum*, may be so abundant in grain fields as to cause the crop to be graded as smutty.

USTILAGO SHASTENSIS Zundel (Mycob. N.A. 63. 1940. Also Mycol. 43 : 68. 1951)

To complete the picture of the North American reticulate-spored species of *Ustilago* on *Polygonum*, it may be noted that in the type specimen of *U. shastensis* on *P. shastense* Brewer the spores are 7.0–10.5 × 6.5–10.0μ (excluding a few apparently malformed, elongate spores); wall light brownish purple, with meshes 0.2–0.3μ high, 0.7–1.5μ diam. *U. polygoni-punctati*, which also has small spores, has much bolder meshes.

The smuts attacking *Rumex* and *Oxyria* are as complex a group as those attacking *Polygonum*. The writer has not seen adequate material to interpret Liro's (6) treatment of these smuts fully, but the following notes may give partial clarification.

USTILAGO PARLATOREI Fisch. v. Waldh. (Hedw. 15 : 177. 1876)

U. parlatorei was described from *Rumex maritimus* L. in Russia. The spores are spectacularly sculptured, bearing a conspicuous reticulum with a slender spine arising from every node. As Liro points out, in focusing slowly down upon a spore one sees first the delicate spines arranged in hexagonal or pentagonal pattern, and finally the reticulum. The only Canadian specimen seen, presumably of this fungus, is a fragment of a collection from Fort Garry, Man., 22 July 1940 (leg. J. H. Brodie), on *Rumex crispus* L. The fragment consists merely of a sorus on a piece of leaf, but *R. crispus* is abundant in the area and there is no reason to doubt the host determination. The spores are 9.5–13.5 × 8.8–12.5μ; wall deep brownish purple, with meshes 0.4–0.7μ high, 0.9–1.6μ diam., and with a spine 0.7–1.4μ high arising from each node of the reticulum. This fungus agrees well with Liro's description except that the meshes are lower. It is possibly varietally distinct from the smut on *R. maritimus*, which has not been seen.

Fischer (3) gives *U. rumicis* (Berk.) Clint. as a synonym of *U. parlatorei*, but Liro (6, p. 25) indicates that *U. rumicis* is a synonym of *U. kuehniana* Wolff 1874. The latter has slightly larger spores than *U. parlatorei* and has no spines at the nodes of the reticulum.

It should be noted that Ell. & Ev. N. Am. Fungi 2701, issued as *U. parlatorei* on *R. britannica*, is a distinct fungus and that the host is probably *R. orbiculatus* Gray. The spores in this specimen are 12.5–19.5 × 11.2–18.0; wall light brownish purple, with meshes 1.4–2.5μ high, 1.0–2.7μ diam., and without spines at the nodes. This fungus must be called *Ustilago coronata* Liro (Ann. Acad. Sci. Fennicae Ser. A, 17 : 244. 1924) unless some prior name should prove to be applicable.

USTILAGO VINOSA (Berk.) Tul. (Ann. sci. nat., Bot., III, 7 : 96. 1847)

A search in the phanerogamic herbarium of the National Museum of Canada recently yielded three additional records of this systemic smut on *Oxyria digyna* (L.) Hill from Prince Patrick I., Dist. of Franklin; Canol Road, southern Yukon; and near Griffin L., B.C. A specimen on *Rumex arcticus* Trautv. from Bloody Falls, near Coppermine, Dist. of Mackenzie (W. I. Findlay 146) is similar in habit and has indistinguishable spores. It must be assigned to this species although it may be specialized on its host. A composite description from the above and Norwegian material follows: Spores 5.5–11.5 × 5.0–9.8μ; wall light brownish purple, reticulate, with meshes 0.2–0.4μ high, 0.7–1.8μ diam. There appears to be no previous record of a smut on *R. arcticus*.

The remaining group of purple-spored smuts with which we are concerned is that attacking Caryophyllaceae. These smuts are all systemic, but may be placed in two categories according to whether the sori are in the ovaries or the anthers. Four species have been described as attacking the ovaries, *Ustilago duriaeana* Tul. on *Cerastium glomeratum* Thuill., *U. holostei* de Bary

on *Holosteum umbellatum* L., *U. ducellieri* Maire on *Arenaria serpyllifolia* L., and *U. alsineae* Clint. & Zundel on *Stellaria praecox* A. Nels. Specimens examined on *Cerastium brachypetalum* Pers., *Holosteum umbellatum*, and *Arenaria serpyllifolia*, presumably representing the first three species, are almost indistinguishable. Fischer's (3) action in combining them under *U. duriaeana* seems to be justified. A longer series of specimens would be needed to show whether the small differences seen are constant enough to allow the recognition of varieties. A composite description from material examined follows: Spores 10.5–15.0(–16.5) × 10.0–14.0(–16.0)μ; wall brownish purple, reticulate with meshes 0.7–1.8(–2.5)μ high, (0.8–)1.3–2.5μ diam. The smut on *Cerastium* tends to have the largest spores with the boldest reticulation. *U. alsineae* has not been examined, but seems to have somewhat smaller spores and shallower meshes.

The smuts that fruit in the anthers of their hosts have been variously treated as one to many species. American authors have generally recognized one or two species. Liro (6) recognized 11, largely on the basis of inoculation tests. The majority of specimens are generally placed in *U. violacea* (Pers.) Roussel. All these smuts have much shallower reticulation than *U. duriaeana* and slightly to markedly smaller spores. The smuts with the largest and smallest spores are so distinct that one would unhesitatingly place them in separate species if the intermediate material were not known. Unfortunately an adequate series of specimens reveals marked intergradation.

When the measurements of specimens of *U. violacea* (*s.l.*) on the majority of listed hosts are tabulated, most can be fitted into three size groups. The most practical solution seems to be to treat these size groups as varieties, thereby immediately making clear the spore size in any specimen mentioned. The relatively small number that do not clearly fit in one of these varieties can be listed as intermediate between two variteties. A further splitting into forms may be adopted if host specialization is proved. The following arrangement is therefore proposed:

USTILAGO VIOLACEA (Pers.) Roussel (Fl. Calvados, 47. 1806) var. VIOLACEA

Specimens on the type host, *Saponaria officinalis* L., yield spores 6.3–10.0 × 5.5–8.2(–8.8)μ; walls reticulate, with meshes 0.2–0.5μ high, 0.6–1.5μ diam. Specimens examined on *Arenaria groenlandica* (Retz.) Spreng. from New Hampshire, and *Dianthus deltoides* L. from Sweden, fit in this variety. Specimens on *Silene cucubalis* Wibel from Germany, *S. grayii* Wats. from California, *S. maritima* With. from Sweden, and *S. nutans* L. from Sweden all have slightly smaller spores.

USTILAGO VIOLACEA (Pers.) Roussel var. MAJOR Clint. (J. Mycol. 8 : 139. 1902)
(*Ustilago major* Schröt., Die Pilze Schles., 273. 1887)
(*Ustilago clintoniana* Cif., Ann. Myc. 26 : 64. 1928)

Clinton described this fungus as a new variety on *Silene watsonii* Rob., from Washington, choosing, by chance, the same epithet as Schröter had

already used for his fungus on *S. otites* (L.) Sm. Ciferri, in raising Clinton's fungus to specific rank, gave it a new name in the belief that it was distinct from *U. major*. However there seems to be no clear distinction, and the amount of variation between specimens on *S. otites* makes one doubt the wisdom of recognizing it as a species. Spores on *S. otites* are (6.3–)7.0–11.5 (–12.5) × (5.5–)6.0–9.5μ; meshes 0.2–0.5μ high, 0.6–1.6(–1.8)μ diam.

USTILAGO VIOLACEA (Pers.) Roussel var. **stellariae** (Sow.) Savile comb. nov.
(*Farinaria stellariae* Sowerby, Engl. Fungi, Pl. 396, Fig. 1. 1803)
(*Ustilago stellariae* (Sow.) Liro, Ann. Acad. Sci. Fennicae Ser. A, 17 : 39. 1924)

Liro gives *Stellaria alpestris* Hartm. and *S. gramineae* L. as hosts for *U. stellariae* and describes the spores as 4–8μ diam. Only two North American specimens of this smut on *Stellaria* are known to the writer: on *S. calycantha* (Ledeb.) Bong., Kenai L., Kenai Peninsula, Alaska (J. A. Calder 5696); and *S. longipes* Goldie, Yellowknife, Dist. of Mackenzie, N.W.T. (W. J. Cody and B. J. McCanse 3219). These specimens match exactly: Spores 4.8–7.4 × 4.2–6.2μ; with meshes 0.1–0.3μ high, 0.5–1.3μ diam. A Swedish specimen on *S. holostea* L. has slightly larger spores; and one on *S. calycantha* × *longifolia*, also from Sweden, has spores 6.0–9.5 × 4.3–8.0μ, approaching var. *violacea*. It is thus clear that the forms intergrade seriously, although on a given host there usually is marked morphological constancy.

Acknowledgments

The writer's thanks are due to Dr. Geo. W. Fischer for advice on the disposition of *Thecaphora apicis* and for the gift of a slide of *Ustilago punctata* Clint.; and to Dr. Bernard Boivin for assistance in preparing the Latin diagnoses.

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STUDIES IN FOREST PATHOLOGY

XI. DECAY IN BLACK COTTONWOOD IN THE MIDDLE FRASER REGION, BRITISH COLUMBIA[1]

By G. P. Thomas[2] and D. G. Podmore[3]

Abstract

A study of decay of black cottonwood, *Populus trichocarpa* Torr. and Gray, revealed that, although 70 species of fungi caused decay, only six caused significant loss in living trees and that two of these, *Polyporus delectans* Peck and *Pholiota destruens* (Brond.) Quél., caused 92% of this loss. The sporophores and associated decays of certain of the fungi are described and their relative importance is indicated. Data on the relation of decay to tree age showed that, despite a high incidence of infection, the average volume of decay per infected tree was low. In general, decay proved important only to the recovery of specialty products such as plywood. A significant reduction of strength was found to occur in wood containing an early stage of decay caused by *P. destruens*. The practicability of segregating trees having a high or low probability of being decayed was demonstrated through the use of decay indicators.

Introduction

Among the broad-leaved species of forest trees found in British Columbia, black cottonwood, *Populus trichocarpa* Torr. & Gray, today ranks first in value of production and in resource volume. Recently a sustained demand for cottonwood logs has occurred, particularly of a quality suitable for manufacture into plywood, with the result that problems inherent to the utilization of the species have become increasingly evident. In some instances, for example, the irregular occurrence of decay in excessive amounts has prevented the making of accurate forecasts of probable yields from forest stands. Upon request of the British Columbia Forest Service and certain of the forest industries, examinations were made of stands of merchantable-sized trees to determine the degree of loss and the specific fungi that characterize this class of cottonwood. In order that decay incidence and development could be related to the growth characteristics of cottonwood, considerable time was spent in accumulating the growth and yield data essential to this purpose.

Location and Type of Stands Sampled

Sample areas were located close to Quesnel (Fig. 1), within a region supporting the river-margin stands typical of cottonwood growth in British Columbia. The 1947 sample consisted of a single 20-ac. plot, established for the purpose of determining the species of fungi that cause decay in cottonwood. The 1948–49 samples together consisted of a series of 28 contiguous $\frac{1}{4}$ ac. plots, chosen to permit an examination of decay in relation to cottonwood growth and yield.

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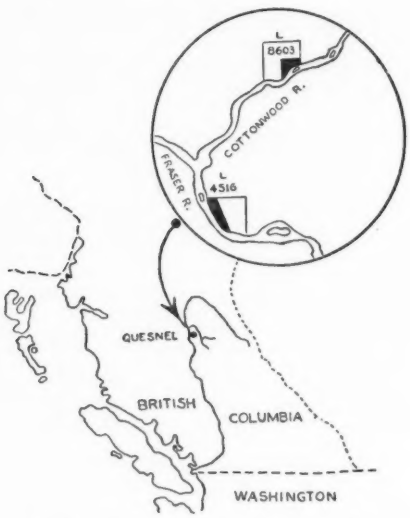

FIG. 1. The location of the areas studied.

Cottonwood stands are normally characterized by the occurrence of trees in even-aged groups, of variable extent, from one part of the stand to another. For this reason it is difficult to sample any one age class to the exclusion of others. This influence was reflected at Quesnel where scattered young and old trees were included in the sample. The basic data for the sample, presented in Table I, indicate the degree of variation that may occur throughout even a small area of cottonwood. A knowledge of decay applicable to a more uniform stand condition than that studied at Quesnel would require a more selective system of sampling than was carried out.

TABLE I

BASIC DATA APPLICABLE TO A 7 AC. SAMPLE OF COTTONWOOD, NEAR QUESNEL, BRITISH COLUMBIA*

Species	Number of trees		Age (years)		Diameter (inches)		Total basal area per acre (sq. ft.)
	Total	Per acre	Average	Range	Average	Range	
Cottonwood	365	52	136	45–197	24	7–48	171.8
Spruce	194	27	109	48–157	11	6–24	18.6
Douglas fir	81	11	130	94–165	13	6–24	12.1
Birch	10	1	—	—	9	6–15	0.5
Total	650	91	—	—	—	—	203.0

* *Includes all cottonwood and all other species 6 in. in diameter, and over, at breast height (4.5 ft.).*

Method of Study

The program of field and laboratory work carried out was that of standard practice (3) at the Victoria Laboratory of Forest Pathology, although some modifications were necessary to obtain data specific to this study. Preliminary emphasis was placed upon identifying the fungi that caused decay, a 20-ac. plot being used for this purpose. Identifications of sporophores and their associated decays, thus obtained, facilitated field identifications during later phases of the work. Interim and final emphasis was placed upon obtaining growth and yield data relative to the incidence, extent, and mode of entrance of the decays. Further studies were made of visible defects that were in some way indicative of hidden decay in trees. A series of 28 one-quarter-acre plots was used for these purposes.

All trees were felled at a height of 2.5 ft. and were cut into lengths that permitted the tracing of decay patterns within trees and logs. The trees were scaled in the field to the extent that measurements were taken of the gross dimensions of logs and defects as they occurred from stump height to a 10-in. top diameter (inside bark). The volume of logs and defects were determined in the laboratory, but logs were graded in the field, as peeler-quality[4] or nonpeeler-quality, according to standards devised for the purpose (Table II).

TABLE II

STANDARDS FOR PEELER-GRADE COTTONWOOD CUT EAST OF THE CASCADE MOUNTAINS IN BRITISH COLUMBIA*

Specification	Value
1. Minimum top diameter	16 in. (inside bark)
2. Minimum log length	9 ft.
3. Normal log length	17 or 26 ft.
4. Random log length	Over 26 ft.
5. Surface defects	Clear of knots and splits
6. Heart rot	If located at the center of a log not to exceed 9 in. in diameter at either end of the log

* *Standards devised in cooperation with the plywood industry for the purpose of this study.*

Early in the study it became apparent that the cultural method of identifying the fungi causing decay was limited in its application to cottonwood. It was usually found impossible to isolate the causal organisms from rot samples, partly because of the frequency of bacterial contaminations in platings from the water-soaked wood and partly because of the extremely slow rate of growth in artificial culture of some of the fungus species concerned. In the hope of increasing the number of isolations from fresh samples, a field laboratory was established at Quesnel, but the percentage of samples from which isolations of the causal fungi was obtained remained low. Hence it was necessary to

[4] *Peeler-quality: logs of sufficient size and surface quality to permit their manufacture into plywood.*

base determinations on the gross appearance of the decays and on the comparison of such decays with other samples associated with known fruit bodies. A considerable portion of the gross volume of decay recorded at Quesnel was identified on this basis, as indicated in Table III.

TABLE III

BASIS FOR THE IDENTIFICATION OF DECAY IN COTTONWOOD AT QUESNEL, BRITISH COLUMBIA*

	Number of infections	Volume of decay (cu. ft.)
Living trees		
Cultures obtained	25	180.6
Associated sporophores	64	381.6
Wood sample comparisons	211	623.6
Field identifications	108	279.7
Totals for living trees	408	1465.5
Dead trees		
Cultures obtained	2	26.5
Associated sporophores	27	1318.4
Wood sample comparisons	29	1126.2
Field identifications	17	600.2
Totals for dead trees	75	3071.3
Totals for all trees	483	4536·8

* *Data obtained from 334 trees 13 in. d.b.h. (o.b.) and over.*

The Growth Characteristics of Cottonwood

Cottonwood is distributed uniformly throughout British Columbia, growing best at low altitudes. Forest stands of the species are confined to newly-formed soils, particularly those of river and lake margins, newly-eroded slopes, and deltas. It also occurs singly, or in small groups, in association with other species. It is shade-intolerant, requires abundant soil moisture throughout the growing season, is even-aged in fully-stocked stands, particularly in the sapling stage, and loses dominance rapidly at maturity to its more shade-tolerant associates.

Maturity of individual trees, expressed by the age at which a decline in the rate of periodic increment becomes evident, occurred beyond 200 years at Quesnel. However, such an index of maturity applies mainly to open-grown trees that do not form a part of continuous, or closed, stands. Consequently, the practical age of maturity for cottonwood, in stand form at Quesnel, was taken to be the age at which the height from ground level to the base of the living crown attained its maximum value, such heights being equivalent to the merchantable lengths of trees. On this basis maturity occurred at 180 years.

Mature cottonwood has a thick, deeply-furrowed, hard-textured bark that is gray at the surface and brick-red within. The stem tapers only slightly, is without branches for over one-half its length, and divides abruptly into large branches in the crown. The crown is broad in open stands, persistent branches

extending downward at least one-half the bole length. In closed stands the crown is narrow and persistent branches extend only rarely into the lower two-thirds of the bole. The wood is straight-grained, odorless, light in weight when dried, and moderately weak and soft. The sapwood is white to pale-yellow in color and is irregular in depth, varying from 1 to 4 in. in a single cross-section of the bole. The heartwood varies in color from buff to dark-brown to almost black. The basic growth and yield data for the Quesnel sample are presented in Table IV.

TABLE IV

GROWTH AND YIELD CHARACTERISTICS FOR COTTONWOOD IN THE QUESNEL REGION, BRITISH COLUMBIA

(Curved values)

Total age (years)	Diameter at breast height (in.)	Height to the base of crown (ft.)	Gross volumes from stump height* to a 10-in. top diameter	
			(f.b.m.)	(cu. ft.)
80	15	52	235	44
90	17	56	295	54
100	19	60	365	64
110	20	62	450	76
120	22	64	545	89
130	23	67	655	105
140	25	69	780	123
150	26	70	935	146
160	28	71	1110	173
170	29	72	1310	200
180	31	73	1520	225
190	32	73	1720	250
200	33	73	1920	273

* *Volumes according to British Columbia scale and Smalian's formula.*

The Decays of Cottonwood

General

The incidence and development of decay in cottonwood are favored by certain of its growth characteristics, chief among which are: its lack of response to release after prolonged suppression and the consequent low vigor of many trees in the stand; its habit of forming large branches that are subject to breakage; its apparent slowness to heal scars that expose the wood; and the high moisture content of its entire woody tissue. Cottonwood logs remain very moist for long periods even when exposed to conditions favorable to drying and, furthermore, the end surfaces of logs are subject to serious checking when drying. Such checks permit easy access into logs for the spores of decay-producing fungi. The combination of these natural characteristics established cottonwood as susceptible to a high incidence of infection and to rapid development of decay once it is initiated.

Relative Importance of the Fungi that Caused Decay

Twenty genera and 70 species of fungi caused decay in cottonwood, only a few of which appeared to affect cottonwood utilization. A list of these fungi is presented in Table V.

TABLE V

A LIST OF FUNGI ASSOCIATED WITH DECAY IN COTTONWOOD IN BRITISH COLUMBIA

Aleurodiscus roseus (Pers. ex. Fr.) Höhn. and Litsch.
Armillaria mellea (Vahl ex Fr.) Quél.

Coprinus sp.

Corticium analogum (Bourd. and Galz.) Burt

C. contiguum Karst.
C. expallens Bres.
C. galactinum (Fr.) Burt
C. laeve Pers.
C. porosum Berk. and Curt.
C. tuberculatum Karst.
C. vellereum Ell. and Cr.

Daedalea confragosa (Bolt.) Fr.
D. unicolor (Bull.) Fr.

Eichleriella spinulosa (Berk. and Curt.) Burt

Fomes fomentarius (L. ex Fr.) Kickx
F. igniarius (L. ex Fr.) Gill.
F. pinicola (Sw.) Cke.

Ganoderma applanatum (Pers.) Pat.

Hericium laciniatum Leers ex Bank.

Merulius confluens Schw.

Odontia sp.

Pellicularia isabellina (Fr.) Rog.

Peniophora aspera (Pers.) Sacc.
P. aurantiaca (Bres.) Höhn. and Litsch.
P. byssoides (Pers. ex Fr.) Bres.
P. carnosa Burt
P. cremea (Bres.) Sacc. and Syd.
P. longispora (Pat.) Höhn.
P. mutata (Peck) Höhn. and Litsch.
P. sambuci (Pers.) Burt

Phlebia merismoides Fr.
P. strigoso-zonata (Schw.) Lloyd

Pholiota destruens (Brond.) Quél.
P. mutabilis (Schaeff. ex Fr.) Quél.
P. spectabilis (Fr.) Quél.

Pleurotus albolanatus Peck
P. lignatilis (Pers. ex Fr.) Gill.
P. ostreatus (Jacq. ex Fr.) Quél.
P. subareolatus Peck
P. ulmarius (Bull. ex Fr.) Quél.

Polyporus adustus Willd. ex Fr.
P. delectans Peck
P. dichrous Fr.
P. elegans (Bull.) Fr.
P. glomeratus Peck
P. hirsutus Wulf. ex Fr.
P. melanopus (Sw.) Fr.
P. pargamenus Fr.
P. picipes Fr.
P. pubescens Schum. ex Fr.
P. rutilans Pers. ex Fr.
P. squamosus Huds. ex Fr.
P. subchartaceus (Murr.) Overh.
P. tulipiferus (Schw.) Overh.
P. versicolor L. ex Fr.

Poria aneirina (Sommerf.) Cke.
P. corticola (Fr.) Cke.
P. ferrea (Pers.) Bourd. and Galz.
P. ferruginosa (Schrad. ex Fr.) Karst.
P. griseoalba (Peck) Sacc.
P. obliqua (Pers.) Karst.
P. xantha (Fr.) Cke.

Stereum fasciatum Schw.
S. purpureum (Pers.) Fr.
S. rufum Fr.

Trametes hispida Bagl.
T. mollis (Sommerf.) Fr.
T. tenuis Karst.

Trechispora brinkmannii (Bres.) Rog. and Jacks.

Considering only trees of merchantable size[5], very few species caused measurable volumes[6] of decay. Living trees of this class sustained losses attributed to 4 genera and 6 species, while 7 genera and 13 species of fungi caused decay in dead trees. The relative importance of these fungi, from the points of view of abundance and amount of damage caused, is presented in

[5] *Trees 13 in. d.b.h. (o.b.) and larger.*
[6] *Not less than 0.1 cu. ft.*

Tables VI and VII. The dominance of *Polyporus delectans* Peck and *Pholiota destruens* (Brond.) Quél. in both living and dead cottonwood is thus clearly indicated. The absence of *Fomes igniarius* (L. ex Fr.) Gill. on cottonwood, its abundance throughout the sample area in Sitka alder, *Alnus sinuata* (Regel) Rydb., and its presence on aspen, *Populus tremuloides* Michx., adjacent

TABLE VI

THE INCIDENCE OF INFECTION IN COTTONWOOD AT QUESNEL, BRITISH COLUMBIA*

Species	Living trees		Dead trees		All trees		
	Meas. volumes	Trace volumes	Meas. volumes	Trace volumes	Meas. volumes	Trace volumes	Total infections
Polyporus delectans	149	56	17	4	166	60	226
Pholiota destruens	109	48	19	1	128	49	177
Stereum purpureum	1	25	3	—	4	25	29
Polyporus adustus	2	1	14	—	16	1	17
Armillaria mellea	8	1	3	—	11	1	12
Pholiota spectabilis	5	1	1	—	6	1	7
Ganoderma applanatum	—	—	4	—	4	—	4
Fomes pinicola	—	1	2	—	2	1	3
Pleurotus ostreatus	—	—	2	—	2	—	2
Fomes fomentarius	—	—	2	—	2	—	2
Poria obliqua	—	1	1	—	1	1	2
Pleurotus subareolatus	—	—	1	—	1	—	1
Polyporus glomeratus	—	—	1	—	1	—	1
Totals	274	134	70	5	344	139	483

* *Includes trees 13 in. d.b.h. (o.b.) and over.*

TABLE VII

THE RELATIVE IMPORTANCE OF THE FUNGI THAT CAUSED DECAY IN COTTONWOOD OF MERCHANTABLE SIZE AT QUESNEL, BRITISH COLUMBIA

(Volumes in cubic feet)

Fungi	All trees		Living trees		Dead trees	
	Decay volume	Percentage of total	Decay volume	Percentage of total	Decay volume	Percentage of total
Polyporus delectans	1670.9	36.8	731.7	49.9	939.2	30.6
Pholiota destruens	1388.7	30.6	613.0	41.8	775.7	25.3
Ganoderma applanatum	455.0	10.0	0.0	0.0	455.0	14.8
Polyporus adustus	332.0	7.3	33.8	2.3	298.2	9.7
Stereum purpureum	217.0	4.8	0.4	0.0	216.6	7.1
Polyporus glomeratus	102.8	2.6	0.0	0.0	102.8	3.3
Armillaria mellea	86.2	1.9	44.7	3.1	41.5	1.4
Fomes pinicola	84.8	1.8	Trace*	0.0	84.8	2.7
Pleurotus ostreatus	84.0	1.8	0.0	0.0	84.0	2.7
Pholiota spectabilis	33.7	0.7	33.6	2.3	1.1	0.0
Fomes fomentarius	33.1	0.7	0.0	0.0	33.1	1.1
Poria obliqua	24.5	0.5	8.3	0.6	16.2	0.5
Pleurotus subareolatus	23.1	0.5	0.0	0.0	23.1	0.8
Totals	4536.8	100.0	1465.5	100.0	3071.3	100.0

* *Trace—less than 0.1 cu. ft.*

to the sample area was noted with interest. Important among the fungi that appeared to be essentially saprophytic were *Ganoderma applanatum* (Pers.) Pat., *Polyporus adustus* Willd. ex Fr., and *Stereum purpureum* (Pers.) Fr. Although *Polyporus adustus* and *Stereum purpureum* were both present in living trees, they were associated in all cases with exposed and dead wood, both fungi causing saprots.

Decay and Sporophore Descriptions

Polyporus delectans (Figs. 3, 4, 11, 12)

Together with *Pholiota destruens* this fungus caused most of the decay in both living and dead trees at Quesnel. Prior to this study the fungus had been recorded mainly as a saprophyte on broad-leaved trees and occasionally as causing decay in living trees (7, 8, 12, 13, 15). There are apparently no records to indicate that *Polyporus delectans* causes decay in living trees to the extent recorded at Quesnel. The infrequent occurrence of its sporophores on living trees may account for its obscurity.

The decay occurred mainly as a trunk rot and only rarely as a butt rot. In living trees the rot was confined to heartwood while in dead trees it occurred in sapwood, but only after decay in adjacent heartwood was well advanced. The decay was usually in pockets of variable size and extent and was associated almost invariably with branch stubs or branch scars. When infections were frequent the pockets coalesced to form a decay column. In such cases a cavity was usually present at some point in the decay column. Decay was apparent first as buff to light-brown streaks in the infected wood. As the decay process advanced infected wood became medium-brown in color and sometimes had dark-brown or red streaks scattered throughout. An appreciable loss in wood strength was apparent at this stage. Infected wood gradually became uniformly dark-brown and sometimes laminate, but more often stringy, in texture. In its final stages of decay the wood was dark-brown in color, light in weight, and, where desiccation had occurred, shrinkage cracks were present on both radial and tangential surfaces.

The annual sporophores were sessile and varied from imbricate to effused–reflexed, occasionally to resupinate. They varied in size up to 12 in. broad, 8 in. deep, and 2 in. thick. Both surfaces were pure white when fresh and became tan to brown on drying. The context was white and fleshy when fresh, becoming hard when dried. The fungus fruited readily from mid-July until late summer on log ends or at broken points on trees. A more detailed description of the fungus is given by Lowe (6).

Pholiota destruens (Figs. 5, 6, 13, 14)

This fungus caused more loss than any other species, not only by reason of the actual volume of decay associated with it but also because of its normal occurrence in decay columns and as a butt rot. Volumetric studies of the decay caused by *Pholiota destruens* are not apparent in the literature, although Cartwright and Findlay (2) state that the fungus is common in old poplar

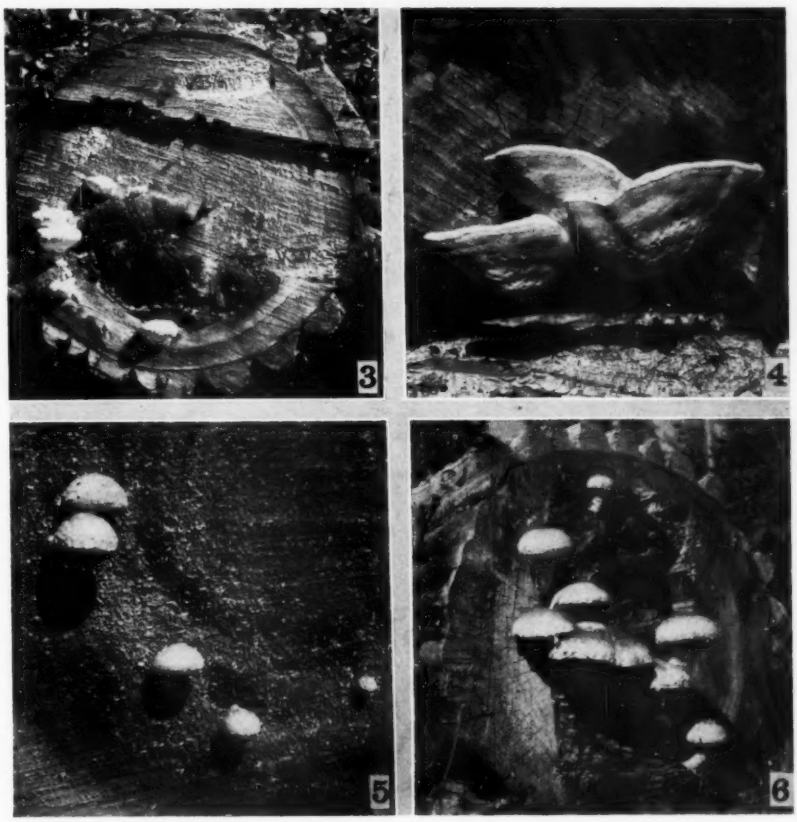

FIG. 3. *Polyporus delectans:* immature fruit bodies and associated decay. × approx. 0.10. FIG. 4. *Polyporus delectans:* mature fruit bodies. × approx. 0.30. FIG. 5. *Pholiota destruens:* immature fruit bodies and associated decay. × approx. 0.25. FIG. 6. *Pholiota destruens:* fruit bodies in various stages of development up to maturity. × approx. 0.15.

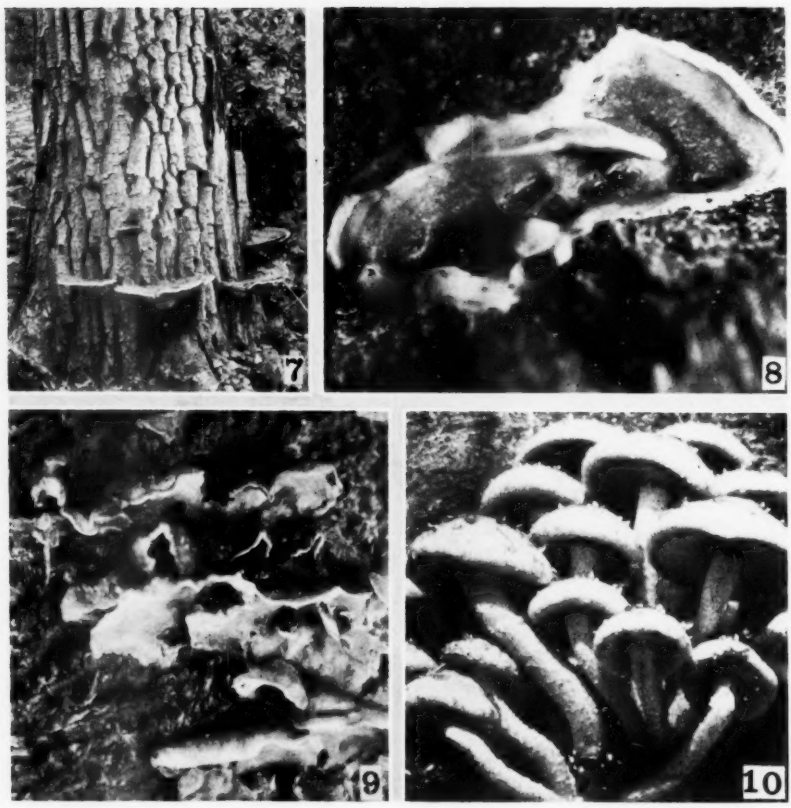

FIG. 7. *Ganoderma applanatum:* mature fruit bodies near the ground line of a dead tree. × approx. 0.07. FIG. 8. *Polyporus adustus:* mature fruit body. × approx. 1.50. FIG. 9. *Stereum purpureum:* mature fruit bodies. × approx. 1.35. FIG. 10. *Armillaria mellea:* mature fruit body cluster. × approx. 0.60.

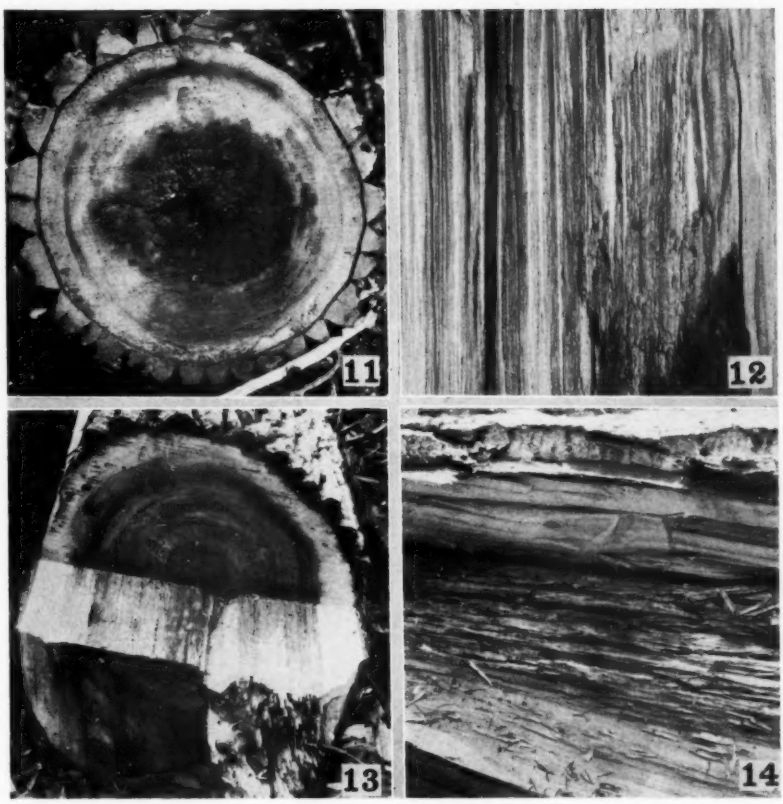

FIG. 11. *Polyporus delectans:* all stages of decay in transverse section. × approx. 0.10. FIG. 12. *Polyporus delectans:* all stages of decay in radial section. × approx. 0.25. FIG. 13. *Pholiota destruens:* incipient and intermediate decay in transverse section. × approx. 0.10. FIG. 14. ***Pholiota destruens:*** final decay. × approx. 0.15.

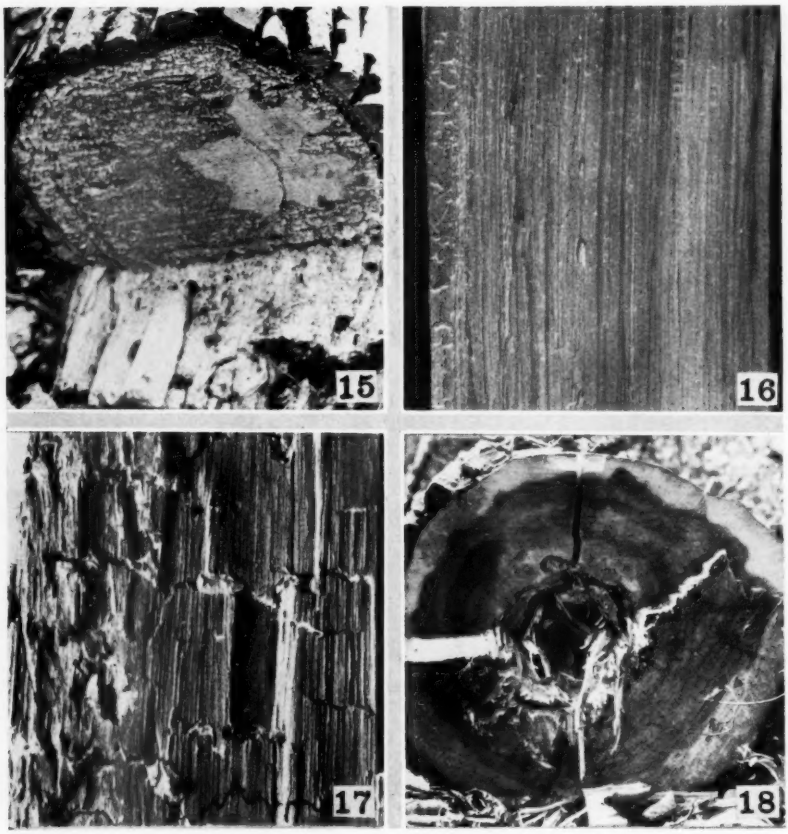

FIG. 15. *Polyporus adustus:* final decay in transverse section. × approx. 0.10. FIG. 16. *Polyporus adustus:* intermediate and late decay in radial section. × approx. 0.40. FIG. 17. *Ganoderma applanatum:* late and final decay. × approx. 0.65. FIG. 18. *Armillaria mellea:* all stages of decay. × approx. 0.08.

trees in which it causes a heart rot. Overholts (11) records the fungus as occurring on stumps and trunks of *Populus* and other deciduous trees. At Quesnel there was no question of its importance as the cause of butt rot of heartwood in living trees. The fungus remains active in dead trees, as does *Polyporus delectans*, but much of the decay associated with it in dead trees undoubtedly occurs prior to death. The fungus seems to remain active in stumps and logs for a few years only.

Initial decay was difficult to detect in dark-colored heartwood but was more obvious in light, or straw-colored, heartwood where it appeared as buff to dark-brown streaks. As decay progressed the stains intensified at first and later the stained areas became bleached, although darkish streaks remained scattered throughout. Small, irregular, white patches gradually appeared, giving the decayed wood a faint white-mottled cast. In the final stages of decay the wood became uniformly yellowish to tan, sometimes darker, and readily separable along the annual rings.

The sporophores grew abundantly, from midsummer to late autumn, at the surfaces of scars or at broken points on living trees and on log ends. The pileus varied at maturity up to 7 in. broad, was fleshy when fresh, dried to tough-leathery, varied in color from tan to brown, and usually showed large white floccose patches on the upper surface. The sporophores, which occurred singly or in clusters, were mostly stipitate but sometimes spatulate. The gills were white at first, becoming dark-brown later. The veil was white, and ruptured to form a pure-white annulus. The stem, when present, varied up to 2 in. thick, was equal or enlarged downward, excentric or central, white to tan in color, and contained a scattering of white scales over its surface. A more complete description of this fungus is given by Overholts (11).

Ganoderma applanatum (Figs. 7, 17)

This fungus has long been known to cause decay in both the heartwood and sapwood of many species of broad-leaved trees, usually in dead trees and less commonly in living trees. It was found at Quesnel only in dead trees but, so extensive was the decay in some of the trees that had died recently, it seemed probable the fungus had been active in living trees.

Initial decay occurred as a bleached zone in infected wood. Zone lines, brown to black in color and of variable width up to one-eighth of an inch, often preceded the advancing zone of decay. Infected wood gradually became white-mottled, particularly on the radial surface, and finally became a white to pale-yellow, soft, wet and spongy mass.

The sporophores grew close to the ground line on dead trees and also on the ends of logs. They were perennial, sessile, varied in shape from applanate to convex, and ranged in size up to 24 in. broad, 16 in. deep, and 3 in. thick. The upper surface was thick, hard, smooth, irregularly zonate, gray to black in color, and was dusted frequently with a thick coating of reddish-brown spores. The pore surface was uniformly white when fresh, became brown if bruised, and dried to pale-yellow.

Polyporus adustus (Figs. 8, 15, 16)

This fungus has been reported many times as the cause of decay in dead trees, in logs, and in logging debris (4, 6, 9). It was observed at Quesnel as the cause of decay in both dead and living trees but, when present in living trees, it was always associated with trunk scars. In no case was the fungus observed causing decay in living sapwood.

The decay appeared first as a tan to yellow stain which was evidently not accompanied by loss in wood strength. Conspicuous white mottling preceded the final stage of decay which was pale-yellow in color, punky in texture, light in weight, and moderately dry. Narrow and distinct black to brown zone lines were randomly distributed throughout the decayed wood.

The annual sporophores were sessile and varied from imbricate to effused–reflexed to resupinate. They grew on exposed sapwood of dead trees, on logs, and on logging debris. The upper surface varied from white when young to tan or gray when older, was finely-hairy when young, and was zonate to azonate. The pore surface was gray to black and had a thin sterile margin. The context was thin, white, and fleshy at first, becoming tough when dried.

Stereum purpureum (Fig. 9)

This fungus was observed frequently on the faces of exposed sapwood on living trees and on log ends. Prior to the Quesnel study it was recorded by Graham (4) and Cartwright and Findlay (2) as being found on stumps and logs of poplars and birch and as the cause of a rot in felled timber. The fungus was associated with decay at Quesnel in trace amounts (less than 0.1 cu. ft. per infection) in most cases. It was apparent that if logs are moved from felling areas soon after trees are felled very little decay will result from this fungus. Cartwright and Findlay (2) suggest that immediate removal of logs from felling areas and the use of water storage until the logs are required for manufacture would be a practical method of preventing damage by this fungus.

The decay appeared first as a pale-brown stain, at which stage the decayed wood was not noticeably weakened. Advanced decay was rare in logs other than in culls and in logging debris. The incipient stains gradually disappeared and infected wood became bleached. In the final stage of decay the wood was light in weight, moderately dry, and varied in color from white mottled to pale-yellow.

The annual sporophores varied in size up to 1 in. in width. They grew profusely from mid-July until late autumn, developing best in reduced light. They were sessile and effused–reflexed to resupinate. The upper surface was gray to buff in color, usually narrow, and densely hairy. The hymenium was even, smooth, purplish at first, becoming buff to brown later.

Armillaria mellea (Figs. 10, 18)

This fungus causes decay in both coniferous and broad-leaved trees (5, 10, 14). Living and dead trees are equally susceptible. At Quesnel it caused a heart rot in the butt section and in the roots of living trees. In dead trees it caused

both a heart rot and sap rot. The decay was unimportant at Quesnel, except by reason of its location in the butt section of trees, only 13 trees being infected.

The decay appeared first as a tan to brown stain which went unobserved in dark-colored heartwood. As the decay progressed, the wood became bleached and later became mottled by reason of large, irregular, confluent patches of white material that were scattered throughout the straw-colored wood. In its final stage of decay the wood was soft, stringy, white to yellow in color, and had thin wefts of brown to black lines of mycelium scattered throughout. A conspicuous feature of this fungus is the presence of subcortical and subterranean rhizomorphs (1).

The sporophores are mushrooms and they grew either singly or in clusters from a common base, emerging from the soil above infected roots or at the bases of trees. The pileus was fleshy, convex at first becoming somewhat flattened later, reached a diameter up to 6 in., varied in color from yellow to buff to brown, and was dotted with dark-brown scales. The stalk was central, up to 10 in. long, and was enlarged downward to a slight degree. It was yellowish in color and sometimes bore a white annulus.

Decay Relations

General

In addition to determining the specific fungi that caused decay in cottonwood and their relative importance as the cause of cull in trees, some more practical interpretation of the significance of decay in cottonwood was sought.

TABLE VIII

THE INCIDENCE OF INFECTION IN LIVING COTTONWOOD AT QUESNEL, BRITISH COLUMBIA*

(Curved values)

Age class	Percentage of infection of total trees in age class	
	Trees with measurable decay only	Trees with measurable decay or trace decay
80	32	71
90	36	73
100	41	74
110	46	76
120	51	77
130	57	79
140	64	80
150	71	82
160	74	83
170	76	85
180	77	86
190	77	87
200	77	89

* *Based on 293 trees 13 in. d.b.h. (o.b.) and over.*

Decay was, therefore, examined in relation to certain tree, stand, and wood characteristics. Recognition was given to the fact that in all stands only certain trees become infected. Accordingly, the sample was analyzed to illustrate both decay incidence and the volume of decay associated with infected trees.

The Relation Between Decay Incidence and Age

Living trees of merchantable size were examined to determine the relation between tree age and the incidence of decay. Data were analyzed to show the percentages of trees per age class that may be expected to contain decay in either trace amounts or in measurable volumes (Table VIII).

A high incidence of decay at an early age was indicated for cottonwood, even when only measurable volumes of decay were considered. The marked difference between the incidence of measurable volumes of decay and the total incidence that occurred in the younger age classes became less evident at

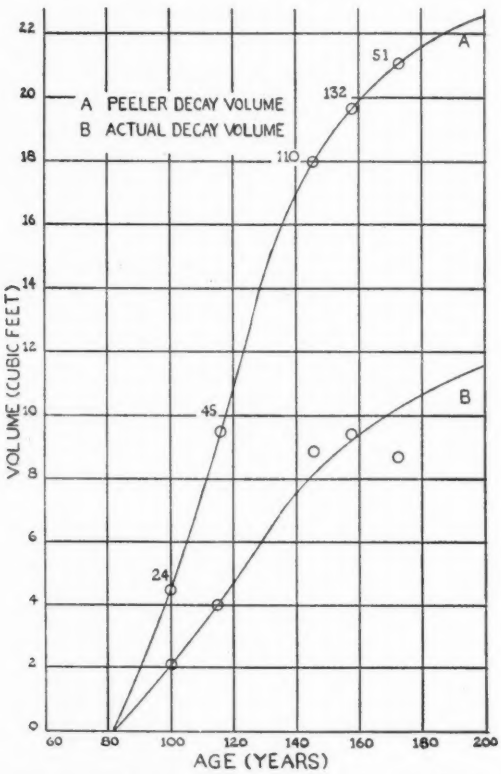

FIG. 2. The relation of tree age to decay volume in infected cottonwood.

about age class 150 years. Considering the incidence of measurable decay volumes alone, a pronounced slowing down of the rate of increase was evident at age class 150 years.

The Relation Between Decay Volume and Age

Living trees with measurable volumes of decay were analyzed to determine the relation between tree age and average decay volume. Recognition was given to the fact that the net recovery of wood was influenced by both the amount and location of decay in trees and logs. Accordingly, two classes of decay were recognized, i.e., actual decay and peeler decay. Actual decay volumes were those based on gross measurements alone. Peeler decay volumes were actual decay volumes plus the sound-wood volumes that were lost to peeler-grade recovery by reason of the location of the decay concerned.

In computing peeler decay volumes a peeler core of 6-in. diameter was accepted as standard. A standard peeler core permitted a 3-in. core of decay at either or both ends of a log, hence, when a core of decay exceeded 3-in. diameter an abnormal peeler core resulted. The difference between a normal peeler core and one of abnormal size formed the basis of peeler decay. When decay exceeded 9-in. diameter the entire contents of the log was culled from peeler-grade utilization. Fig. 2 and Table IX present the results of the analysis.

The analysis indicated a marked difference between actual decay volumes and peeler decay volumes, particularly in the older age classes. However, at no point up to age 200 years did decay increment exceed or equal gross wood

TABLE IX

THE RELATION BETWEEN AGE AND DECAY VOLUME IN COTTONWOOD AT QUESNEL, BRITISH COLUMBIA*

(Curved values)

Age class	Actual decay		Peeler decay	
	Decay volume	Decay increment	Decay volume	Decay increment
80	Trace	—	Trace	—
90	0.9	0.9	2.0	2.0
100	2.1	1.2	4.5	2.5
110	3.4	1.3	7.5	3.0
120	4.7	1.3	10.8	3.3
130	6.2	1.5	14.4	3.6
140	7.6	1.4	17.0	2.6
150	8.6	1.0	18.7	1.7
160	9.4	0.8	19.9	1.2
170	10.1	0.7	20.8	0.9
180	10.6	0.5	21.6	0.8
190	11.1	0.5	22.2	0.6
200	11.6	0.5	22.6	0.4

* *Based on 185 trees 13 in. d.b.h. (o.b.) and over that contained measurable volumes of decay. Volumes are cubic feet according to Smalian's formula.*

increment. The point of maximum decay increment for both types of decay was reached at age 120-130 years in contrast with the age of maximum wood increment which was 150-160 years (Table IV).

The Relation Between Decay and the Strength Properties of Cottonwood

A loss in wood strength is generally evident when decay is present. Less evident, however, is an appreciation of when strength loss first becomes pronounced in the decay process. Since wood strength is of major importance in peeler-grade cottonwood it was desirable to learn at what stage in decay development loss in wood strength first becomes pronounced. Time and facilities permitted tests being conducted on wood infected by only one major decay fungus, *Pholiota destruens*.

Test material was obtained from trees containing all stages of decay caused by *P. destruens*. Areas of decay within each block of test material were recorded as zones *A*, *B*, and *C*, respectively representing a transition from initial decay through areas of possible initial decay to areas of presumed sound wood. Test sticks of uniform dimensions were obtained from the blocks and zones for testing of crushing strength parallel to the grain[7]. The results of these tests are presented in Table X.

TABLE X

THE AVERAGE CRUSHING STRENGTH PARALLEL TO THE GRAIN FOR COTTONWOOD CONTAINING THE INITIAL STAGES OF DECAY CAUSED BY *Pholiota destruens*

(Pounds per square inch)

Block number	Zone*			Reduction C to A
	A	B	C	
1	1916	2057	2198	282
3	2057	2142	2107	50
4	1956	1925	1969	13
5	1817	2045	1963	146
6	2014	1947	2094	80
7	1884	1988	1933	109
9	1900	2097	2191	291
10	2005	1975	2171	166
11	1460	1516	1762	302
12	—	1409	1786	377
13	1179	1477	1541	362
Zone average	1852	1916	2003	151

* *Zones A, B, and C represent respectively areas of decay, possible decay, and presumed sound wood.*

[7] *The tests of wood strength were carried out through the courtesy of Mr. J. B. Alexander, Senior Engineer, Timber Mechanics Section, Vancouver Laboratory, Forest Products Division, Department of Resources and Development.*

The differences between zone averages are believed to be substantially indicative of strength reduction in wood containing the early stages of decay caused by *Pholiota destruens*. These differences might be expected to be even more pronounced were tests of strength other than that of crushing strength parallel to the grain carried out, for it is believed that strength measured in compression parallel to the grain is affected the least in the early stages of decay (1). Zone variations between blocks were attributed partly to the difficulty of selecting blocks in the field that contained decay in exactly the same stage of development.

The Relation Between Decay and Tree Abnormalities

The lack of visible evidence of the occurrence of decay in cottonwood trees makes it difficult to form an estimate of the pathological condition of forest stands. Consequently, some method of detecting decay that would be applicable to standing timber was sought.

Data were taken over a 4-ac. plot at Quesnel in an attempt to correlate the presence of tree abnormalities with the occurrence of decay. An examination of 194 living trees on this plot yielded seven categories of visible tree abnormalities, in addition to sporophores, that were associated directly and consistently with decay (Table XI).

TABLE XI

THE COMPARATIVE EFFECTIVENESS OF VISIBLE DEFECTS AS INDICATORS OF HIDDEN DECAY IN COTTONWOOD AT QUESNEL, BRITISH COLUMBIA

Defect	Frequency of occurrence			Percentage with decay
	Decay present	Decay absent	Total	
Basal scars	35	2	37	95
Branch stubs	36	6	42	86
Broken tops	3	—	3	100
Bunch-knots	10	2	12	83
Butt swell	2	—	2	100
Crook	27	6	33	82
Trunk scars	10	1	11	91
Totals	123	17	140	88

On the basis of the defects listed in Table XI a system of tree classification was devised and was correlated with a volumetric analysis of the sample. Three categories of trees were recognized, Residual, Suspect, and Dead. Residual trees were trees of merchantable size that exhibited no single indicator of hidden decay. Suspect trees were trees of merchantable size that exhibited one or more indicators of hidden decay. Dead trees were trees that were completely devoid of green foliage. The basic results of the application of the tree classification system are presented in Table XII.

TABLE XII

THE COMPARATIVE EFFECTIVENESS OF TREE CLASSES IN EXPRESSING HIDDEN DECAY IN COTTONWOOD AT QUESNEL, BRITISH COLUMBIA

Tree class	Number of trees	Percentage of total trees	Percentage of gross decay volume	
			In living trees	In all trees
Residual	56	29	13	5
Suspect	117	60	87	39
Dead	21	11	—	56
Total	194	100	100	100

The data presented in Tables XI and XII are intended to express only the principles of tree classification. It should be recognized, when applying a tree classification system, that some portion of the gross volume of decay in stands will remain hidden with no outward indication of its presence. In this respect a tree classification does not permit an exact measure of decay but serves to refine what can, at best, be only an estimate. The segregation of 87% of the decay that occurred in living trees at Quesnel into the Suspect class illustrates a practical refinement of decay estimation in which only 13% of the gross volume of decay in living cottonwood remained undetectable.

Discussion

The scattered distribution of cottonwood permits selection of study areas representative of a wide range of climatic conditions under which the species grows, and for this reason the Quesnel region was selected for study as representing approximately average conditions for cottonwood growth in British Columbia. The even-aged characteristic of cottonwood stands necessitated establishing sufficient plots to permit an examination of a representative range of age groups. In this connection the results of the study of cottonwood growth, which indicated that the species matures at approximately 180 years and reaches its maximum rate of increment at approximately 130 years, permitted confining the sample to stands of 200 years and younger. Extending the basic sample was considered to be beyond the scope of the present study, but is recommended as necessary to the application of the results of this study to conditions not fully represented by the Quesnel sample.

The demonstrated association with decay in living cottonwood of only six species of fungi in four genera does not preclude the possibility that one or more of the additional species that were found to cause decay in dead material may cause rot in living trees. Recognition should be given to the restricted volumetric sample obtained and full allowance should be made for the potential occurrence of decay patterns different from that which occurred at Quesnel, where *Polyporus delectans* and *Pholiota destruens* predominated.

The absence of decay or its presence in many trees in only trace amounts necessitated an analysis of the sample on the basis of the incidence of infection and the average volume of decay in infected trees. In the application of the results of these analyses it should be recognized that the average volumes of decay determined can be applied only to that portion of the stand estimated to contain decay in measurable amounts. The incidence of decay in living trees was high, but the average volume of decay per infected tree was not excessive below age-class 180 years, although in dead trees both incidence of infection and average volume of decay were high. On this basis dead trees do not yield sufficient sound wood to justify their inclusion in stand inventories. In the case of living trees it is doubtful that decay alone will constitute a major problem, although it has been demonstrated that occasionally logs are culled in plywood utilization on this account and that decay frequently increases the volume of cull in peeler-quality logs by reason of its location within them.

The use of visible tree defects as a method of estimating the presence of decay was demonstrated to be of value for the Quesnel sample. In addition to sporophores, seven classes of defects were established as reliable indicators of hidden decay and were incorporated into a tree classification which was based on the occurrence of one or more indicators on individual trees. Although use of indicators seems to provide a practical method of segregating trees into groups having different pathological ratings, it was evident that only very few defects indicate hidden decay consistently. An example of misuse of defects as decay indicators is the use of "sweep" which proved to be entirely unreliable at Quesnel. Although sweep is frequently classed as equivalent to "crook" as a natural defect, it is entirely unrelated to crook as an indicator of decay, for each defect differs in its origin. Crook proved reliable as an indicator of decay in cottonwood. In the case of scars, broken tops, and branch stubs, unless sufficient time has elapsed since their occurrence as indicated by weathering, these defects did not indicate hidden decay.

The predominance of *Polyporus delectans* and *Pholiota destruens* at Quesnel was demonstrated by associating with these species over 90% of the gross volume of decay found in living trees. Neither species had been recorded previously as the cause of economic loss of any consequence. Although *P. destruens* caused less decay than *Polyporus delectans*, the occurrence of its associated decay as a butt rot established it as the species most important to the recovery of the high-quality wood normally obtained from butt logs. A reduction of 151 lb. per sq. in. in compression parallel to the grain, from sound wood to wood in an early stage of decay caused by *Pholiota destruens*, and the occurrence of incipient decay far in advance of typical decay further indicated the importance of this species. None of the remaining four species of fungi associated with decay in living trees proved significant, although one of these, *Stereum purpureum*, was associated with much of the decay found in dead trees. This species presented no problem in logs from living trees other than as the cause of a blue stain.

The absence of *Fomes igniarius* from the sample was as outstanding as the importance of *Pholiota destruens* and *Polyporus delectans*. Throughout the sample area this species contributed most heavily to the decadence of Sitka alder, and adjacent to the sample plots it was common in stands of trembling aspen. Extensive scouting in regions beyond Quesnel produced only one incidence of infection by *Fomes igniarius* in cottonwood.

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THE EFFECT OF SOIL MOISTURE ON *FUSARIUM* SPECIES[1]

By R. H. Stover[2]

Abstract

Six species and forms of the genus *Fusarium* show optimum growth and survival in soil at 15% saturation. Optimum soil moisture content for actinomycete growth and survival is similar to that for the *Fusarium* species whereas that for bacteria is at 75% soil saturation. The present studies indicate that *Fusarium* spp. are strongly aerobic and that *Fusarium* populations can be greatly reduced by maintaining the soil in a saturated condition in the absence of hosts.

Introduction

In studies on the effect of environment on fusarioses, considerable attention has been devoted to soil temperature, pH, and texture. In a few instances the importance of soil moisture on disease incidence has been noted. However, relatively little information is available on the effect of soil moisture on *Fusarium* species in the absence of hosts. Since flooding is used to control the wilt disease of banana in Central America, it has been necessary to determine the role of soil moisture in the growth and survival of the causal organism *F. oxysporum* f. *cubense* (E.F.S.) Sny. and Hans. (6). This paper reports similar studies with other fusaria.

Methods

The *Fusarium* species used are listed in Table I. All cultures with the exception of *F. oxysporum* f. *nicotianae* had been maintained in sterile soil to preserve the wild type. Two-week-old cultures of the fungi in 10% corn meal in sand were used to infest an air-dry nonsterile loam soil. This soil consisted of 18% clay, 46% silt, and 36% sand with a pH of 8.0. The soil and inocula were thoroughly mixed and placed in glass tumblers, after which soil moisture contents were adjusted from 15 to 100% saturation by the addition of tap water. At 15 and 25% saturation, no attempt was made to distribute the moisture throughout the tumbler; thus a small moisture gradient was present from top to bottom. The tumblers were closed with wax paper and frequently brought up to weight by the addition of water in order to maintain a relatively constant soil moisture content.

One-gram samples were taken for culturing from the center of the tumblers and diluted 1 : 1000. Six plates containing 1 or 0.5 ml. of this dilution were poured with peptone dextrose agar (pH 6.2) containing rose bengal and streptomycin. Fusarium populations were determined at intervals during a period of four months. Bacterial and actinomycete counts were made on Jensen's medium (4) at a dilution of 1 : 100,000. All counts are expressed per gram of air-dry soil.

[1] *Manuscript received June 1, 1953.*

[2] *Research Department, United Fruit Company, La Lima, Honduras, C.A.*

TABLE I

Fusarium SPECIES USED IN SOIL MOISTURE EXPERIMENTS

Species	Host	Source
F. moniliforme	Corn	Harrow, Ont.
F. graminearum	Corn	Harrow, Ont.
F. oxysporum f. *cubense*	Banana	La Lima, Honduras
F. oxysporum f. *nicotianae*	Tobacco	Lexington, Ky.
F. oxysporum f. *niveum*	Watermelon	Harrow, Ont.
Fusarium sp. B[a]	Common saprophyte from soil	La Lima, Honduras

[a] *Later identified by Dr. W. L. Gordon as F. solani.*

Results

The results are shown in Figs. 1 and 2 and Table II. The fusaria studied have an optimum for growth and survival at a soil moisture content between 15 and 25% saturation. The population trends (Fig. 1) for all six species and forms of *Fusarium* are similar. All species are greatly reduced as the soil moisture is increased from 50 to 85% saturation and are almost nonexistent at saturation. From the average number of fusaria calculated in Fig. 2 and Table II, it appears that the optimum is closer to 15 than 25% saturation. The fusaria population trend shown in Fig. 2 is remarkably similar to that of the actinomycetes with the exception of the greater tolerance of fusaria to soil moisture contents of 75 and 85% saturation. The largest bacterial populations were present at 75% saturation.

TABLE II

Fusarium POPULATIONS PER GRAM AIR-DRY SOIL PRESENT IN MOPALA LOAM SOIL AFTER 107 DAYS AT DIFFERENT MOISTURE LEVELS

	Soil moisture content % of saturation					
	15	25	50	75	85	100
F. oxysporum f. *cubense*	260,960	302,080	174,080	65,390	16,900	0
F. sp. B[a]	391,000	240,000	123,250	52,420	33,790	0
F. moniliforme	34,200	28,080	10,210	14,430	2,100	4,830
F. graminearum	183,060	63,340	13,070	7,740	3,300	850
F. oxysporum f. *nicotianae*	173,280	295,710	111,600	39,390	5,410	4,140
F. oxysporum f. *niveum*	232,000	348,000	177,270	81,740	51,610	4,870
Calculated average at 107 days	212,416	212,868	101,580	43,518	18,851	2,448
Actual average of all fusaria in soils when mixed after 107 days	181,440	141,600	50,510	32,900	23,360	770

[a] *All species except* B *are parasitic; Fusarium sp.* B *was later identified as F. solani.*

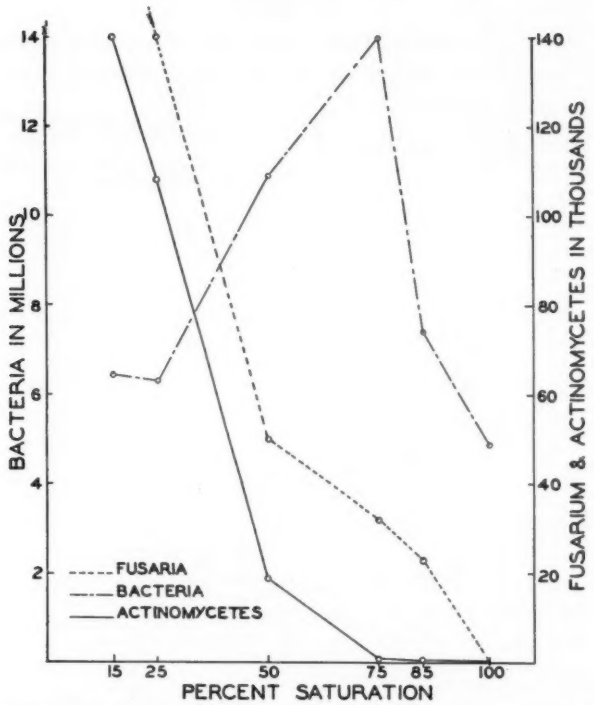

FIG. 1. The effect of different soil moisture contents on six species and forms of *Fusarium*. The points are plotted from the average population of four soil samples taken during a 50-day period beginning 25 days after the experiment was begun.

An interesting observation was the prevalence of *Cephalosporium* spp. in the saturated soil series. Morphologically it is difficult to distinguish this genus from certain fusaria. It appears that some species of *Cephalosporium* are capable of growing in saturated soils where it is difficult for fusaria to survive. Whether or not this characteristic can be used to differentiate certain borderline species in the genera remains to be determined.

Discussion

The six species and forms of *Fusarium* tested have an optimum soil moisture content for growth and survival at or near 15% saturation. At soil moisture levels above 25% saturation, fusaria populations fell off sharply. These data support Garrett's (3) statement that fungi in general, including the root-infecting types, are strong aerobes. Nevertheless, future work will show that some soil fungi, particularly certain species of *Penicillium*, *Aspergillus*, *Cephalosporium*, and *Sporotrichum* are highly tolerant of submerged soil conditions where *Fusarium* spp. are soon eradicated. In Table III are shown

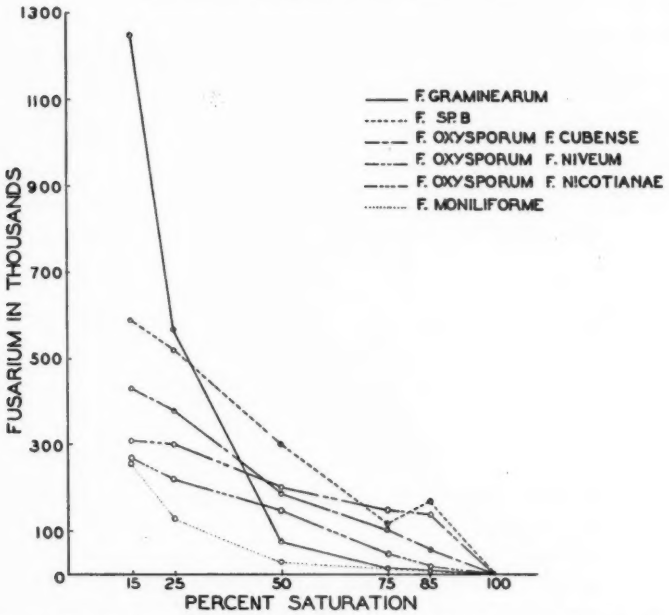

FIG. 2. Populations of bacteria, actinomycetes, and fusaria present in loam soil after 107 days at different moisture levels.

the soil type and moisture effects on various fusarioses. The majority of these diseases are favored by light-textured acid soils and high soil moisture. Since the present and previous studies show that most *Fusarium* species are strong aerobes and favored by low soil moisture contents, it is evident that high soil moisture is exerting a greater effect on the host than on the fungus.

In these studies, the largest bacterial populations were obtained at moisture levels above 50% and approach an optimum at 75% saturation. Also, bacterial populations are known to be far greater in heavy soils than in light-textured soils. Therefore, at low soil moisture and in light-textured soils fusaria would find not only aerobic conditions but less bacterial competition. Thus in sterile soil, the effect of soil moisture on *F. oxysporum* f. *cubense* was much less than in nonsterile soil (6). In fact *Fusarium* growth at 75% saturation in sterile soil was greater than at 25% saturation in nonsterile soil (6), indicating that a competitive bacterial flora at high moisture levels is a factor in reducing *Fusarium* populations. This flora may be in part antagonistic but it is also capable of competing successfully for available oxygen and food. It is possible that a period of soil saturation in the absence of hosts may be utilized to reduce *Fusarium* populations of infested soils to a level where a satisfactory yield of an annual crop could be obtained.

Subramanian (7) found that the disappearance of *F. vasinfectum* from the soil was delayed to a certain extent by anaerobic conditions produced by

TABLE III

EFFECT OF SOIL TEXTURE AND MOISTURE ON VARIOUS DISEASES CAUSED BY FUSARIA

Fungus and disease[a]	Fusarioses favored by		
	Light soil[b]	Low soil moisture	High soil moisture
F. annuum, chili pepper wilt			+
F. oxysporum f. *cubense*, banana wilt	+		+
F. oxysporum f. *lycopersici*, tomato wilt			+
F. orthoceras f. *pisi*, pea wilt	+		+
Fusarium sp., celery yellows			+
F. oxysporum f. *batatis*, stem rot of sweet potatoes	+		
F. lucidus, root rot of coconut palms	+	+	
F. noxius, brown root rot of tea and rubber	+		
F. vasinfectum, cotton wilt	+		+
Fusarium sp., pea collar rot	+		
F. lini, flax wilt	+		
F. nivale, turf snowmold (2)			+
F. orthoceras, lentils wilt (1)	+	+	
F. culmorum, on Marquis wheat (5)		+	+

[a] *Data from Garrett (3) with exception of (2), (1), and (5).*

[b] *No fusarioses appear to be favored by heavy textured soils which generally are alkaline contrasted with the more acid light soils.*

completely saturating the soil but was accelerated by 30% saturation. These findings are contrary to data presented in this paper which indicate the adverse effect of high soil moisture content on the six species and forms of *Fusarium* studied. The conflicting results may be caused by different methods of determining the *Fusarium* populations in the soil. Subramanian used a root colonization method of determining *Fusarium* survival whereas a direct plating method was used in the above studies. When Subramanian used the Cholodny method of observing *F. vasinfectum*, he found the rate of fungus decomposition increased progressively with the addition of moisture up to 90% saturation.

The similar response to soil moisture by the wide range of *Fusarium* species used in this study suggests that corresponding results might be obtained with most species of the genus *Fusarium*.

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